RESPONSES OF SAVANNAS TO STRESS AND DISTURBANCE
A Proposal for a collaborative Programme of Research

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RESPONSES OF SAVANNAS TO STRESS AND DISTURBANCE

A Proposal for a Collaborative Programme of Research

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SECTION I: INTRODUCTION AND OBJECTIVES

OVERVIEW

This document represents a proposal for a programme of collaborative research on tropical savanna ecosystems. Our concern stems from the current trend of degradation in savannas around the world, involving changes in composition and productivity that are adversely affecting the capacity of these systems to support humans and other organisms. In order to arrest or reverse these changes we need to improve our understanding of savanna dynamics under prevailing and projected patterns of land use. Therefore, the objective of this programme is:

To develop a predictive understanding of the ways in which savannas respond to natural and man-made stresses and disturbances.

This can best be achieved through a comparative, intercontinental analysis of some selected aspects of tropical savannas involving a diversity of research inputs.

Over the past few years there have been several syntheses of the results of research on savannas in different parts of the world (Hills and Randall, 1968; Bourlière and Hadley, 1970; UNESCO, 1979; Walker, 1979; Huntley and Walker, 1982; Bourlière, 1983; Sarmiento, 1984). Although these authors do not agree on all points, the syntheses provide a foundation on which to build. Some of the disagreements stem from different concepts as to what constitutes a savanna, others from the different approaches and methods used in these separate research programmes. An international collaborative research programme involving carefully planned comparative studies with a common aim and approach offers the best opportunity for resolving these conceptual differences and gaining the insights that are so urgently needed as a basis for the rational use and management of savannas.

While the scientific results are important in their own right, it is vital that the major insights and findings of the programme should ultimately be applied to the problems of savanna utilization and management. It is not enough to suppose that the findings published in the scientific literature will be picked up and applied by decision makers and managers, or that they will be useful to them in
that form. A more active extension policy is therefore envisaged in which land managers and extension officers will be involved in the programme at an early stage, both to help evaluate the significance of results as they appear, and to assist in developing strategies for translating research results and emerging concepts into management decisions and actions in the field.

DEFINITIONS

Savanna

For the purposes of this programme, core savannas will be defined very broadly to include all those tropical and some near-tropical ecosystems characterized by a continuous herbaceous cover consisting mostly of heliophilous C4 grasses and sedges that show clear seasonality related to water stress. Woody species (shrubs, trees, palms) occur but seldom form a continuous cover paralleling that of the grassy layer. Marginal savanna systems in which either one of these two vegetation components has an insignificant effect can be included for their comparative value. Savannas encompassed by our definition cover extensive areas of South America, Africa and Australia, and also occur in Central America and India (Figure 1).

Figure 1. World distribution of tropical savannas (from Lamotte and Hadley (1984) after Bourlière (1983))
Stress

In this document we use the word "stress" in its accepted physiological sense to describe a constraining environmental influence that restricts the productivity and efficiency of an individual and, by extension, the ecosystem. Such stresses usually operate when an environmental variable, such as temperature, light, water, nutrients or defoliation, deviates markedly from its normal range of values in the system. Stress is seldom accompanied by mortality. As stress becomes more severe it may cause a disturbance.

Disturbance

As used here, a "disturbance" is a change in the structure of a system which usually affects its functioning. Disturbances are often caused by aperiodic events, such as floods, particularly severe storms, prolonged droughts, excessive herbivory, or activities such as bush-clearing and cultivation. Disturbance may result from one, but more often a combination or sequence of extreme values of environmental variables. These may or may not cause mortality of individuals. Opportunities are created for new individuals of the same or different species to become established. Increasingly, disturbances are the result of human activities.

Stability and Resilience

A stable system is one in which those variables defining the state of the system (eg. species composition, relative abundances, biomass, or production) change little in response to outside pressures such as drought, fire or grazing. If disturbed, they return rapidly to their original values (Walker, 1980). A stable system therefore shows little variability through time in the amounts of its state variables. The distinction between compositional stability (relative constancy of species composition and abundance) and functional stability (relative constancy of the processes maintaining primary production) needs to be emphasized since the two can be negatively correlated (McNaughton, 1977).

A resilient system, on the other hand, is usually not stable and the values of its state variables often change considerably when subjected to outside pressure (Walker, 1980). More importantly, the parameters of the system which influence its dynamics also change, thereby redefining the boundaries within which the system remains attracted to its equilibrium point. As a result, future disturbances of the same type are more easily accommodated (Walker, et al., 1981). In contrast, in a stable system, the parameters of the system do not change with disturbance.
In all of these definitions the question of scale arises. Periodic stress, imposed at regular intervals over a long period of time, eventually assumes the characteristics of a continuous phenomenon, while a continuous stress, seen in the very short term and at a local level, may behave very much as a periodic phenomenon. Whether or not a system is perceived to be in equilibrium often depends on the spatial and temporal scale of observation. For example, considerable short-term fluctuations in species composition or production can be observed at a local scale, giving the impression of instability, but when these are viewed over a longer time period, as part of a larger landscape, they simply appear to be variations around some mean value; the system exhibits dynamic equilibrium. Similarly, changes which are regarded as irreversible at one time scale may exhibit slow recovery over longer periods.

The spatial extent of different phenomena is also important. A herbivore's bite is very localized, a fire may cover hundreds of hectares, while drought is experienced at a regional level or above. Moreover, at a local scale, it is only possible to detect the response of one or a few individuals. As the spatial scale expands, so too does the organizational level at which a response is observed. Given the marked temporal and spatial heterogeneity of savannas, it will be particularly important to choose the appropriate observational scale for the problems being studied.

RATIONALE

Almost one fifth of the world's population live in savannas, many of them in rural societies that depend on subsistence agriculture. Per capita food production is generally low, the result of a variety of environmental, social and economic constraints. Rainfall is highly seasonal and variable, leading often to uneven and unpredictable patterns of primary production. Many of the soils are relatively infertile, particularly in the high rainfall zones. This is reflected in low crop yields and in the poor nutritional quality of natural pastures, especially during the dry season. Consequently, even in areas with a high and relatively constant level of plant production not all the plant matter can be used productively by consumers.

Compounding the effects of these factors is the dual nature of land use in many savanna regions. The most productive lands are often set aside for growing cash crops while the poorer lands are used for local food production. This, combined with the continuing rapid growth of the human population in the tropics, is placing increasing pressure on marginal lands, resulting in many cases in degraded environments, reduced productivity and lower carrying capacities.
There is an urgent need therefore to find alternative models of development designed to increase the satisfaction of human needs without causing a decline in long-term productivity and resilience. To be successful, these programmes need to be based on scientifically sound technologies which take into account the relevant physical, biological and human elements of a system. Unfortunately, our knowledge of these features, particularly their dynamic aspects, is still quite fragmentary. This provides one of the main motivations for this programme.

From both a scientific and land management viewpoint, there are a variety of reasons why tropical savannas are an important research subject. Some of these are:

1. The increasingly intense use of savannas by an expanding human population is resulting in adverse changes to the soil and vegetation. When combined with natural stresses such as drought, these changes are leading to increased erosion and aridification of the soil, followed by famine and human misery. Research into the causes and consequences of these changes in savannas could help alleviate some of the problems in the future.

2. Within the tropics, the coexistence and close interaction of the woody and herbaceous strata makes savannas unique. Both strata are of economic value and a better understanding of their coexistence would contribute to improved management.

3. Savannas are one of the most seasonal of the world's major biomes, experiencing strongly contrasting climatic conditions within a year, as well as high variability between years. They also display "an apparently confusing mixture of communities of various sizes, arranged in different patterns at different scales, and each of which may be changing in both an orderly and disorderly fashion, at different rates" (Walker, 1981: 447). This heterogeneity creates a constantly varying environment for the biota and is probably a major factor in enabling a relatively large number of species and contrasting life forms to coexist. Savannas therefore are ideal systems in which to study how plants and animals cope with the various natural stresses imposed by a variable environment. This would contribute to a better understanding of the effects of man-induced stresses in these and other ecosystems.

4. Fire, frequently associated with human activities, is a prominent feature of most tropical savannas. It affects the functioning of these systems in a variety of ways and interacts with other processes, such as herbivory, nutrient cycling and plant recruitment. Since fire can be managed, a better understanding of its ecological effects, and how these can be integrated with other, less manageable ecosystem processes, would be extremely valuable.
5. In addition to the possible contributions that this programme might make to the better management of savannas, further advances in ecological theory can be expected in view of the uniqueness of the set of ecological interactions that determine the existence of these systems.

APPROACH AND KEY QUESTIONS

The approach of this programme is therefore to develop a collaborative international research effort which, through comparative and individual studies, will improve our understanding of both natural and managed savannas and their responses to different kinds of stress and disturbance. The major problems to be addressed by the programme are encompassed in the following two key questions:

1. What are the structural and functional properties of savannas that render them stable and/or resilient to seasonal and aseasonal natural stresses and disturbance (e.g. fire, drought)?

2. Are there critical limits (i.e. thresholds) of disturbance beyond which savanna ecosystems do not recover after the disturbance factor is removed?

The resolution of the problems calls for answers to two further questions:

3. In which ways (both structurally and functionally), and by how much, do different types of savannas change in response to natural stresses (fire, below-average rainfall, floods, etc.) and natural and anthropogenic disturbance (e.g. prolonged drought, over-grazing, de-bushing, and cultivation) and their interactions?

4. What are the mechanisms that determine the manner and the rates by which savannas respond to and recover from a disturbance?
SECTION II: THE DETERMINANTS OF SAVANNAS

INTRODUCTION

Recent syntheses on the ecology of tropical savannas (Huntley and Walker, 1982; Bourlière, 1983; Sarmiento, 1984; Tothill and Mott, 1985) reveal four principal determinants of savanna structure and functioning: soil moisture, soil nutrients, herbivory and fire. Soil moisture availability and soil nutrient status are the key factors, affecting both the balance between grasses and woody plants and the patterns of primary production and plant quality. These in turn influence the kinds and extent of herbivory, associated animal impacts, and the frequency and intensity of fire. In so doing, the availability of moisture and nutrients and the effects of their interaction are indirectly modified.

A fifth determinant of savanna structure is human activity. Humans have been associated with African savannas for more than two million years (Harris, 1980). Likewise, in Asia, there is evidence of human occupation going back as far as one million years BP. Australia and America were not occupied until much later: about 40,000 yrs BP in Australia, and about 25,000 years BP in South America. These long periods of occupation have had a profound effect on both the structure of savannas and their geographical extent. For example, it is believed that the savannas of the Indian sub-continent are derived primarily from woodlands through the action of humans (Singh, 1976; Singh et al., 1983; Gadgil and Meher-Homji, 1985).

Humans can affect savanna structure either directly, as wood-cutters and cultivators, or indirectly, through their ability to manipulate fire and to influence herbivore numbers and distribution, both by hunting and by introducing and managing domestic animals. In more recent times humans have developed the capacity to bring about rapid and considerable change in savanna structure through mechanical and chemical means. Overall, in many parts of the world today, human activity constitutes the major source of disturbance to savanna systems.

The following account represents a selective review of savanna functioning to provide a background for the hypotheses which follow. In this review, we wish to emphasize the composite nature of the main determinants, each of which comprise a number of rather weak but highly interactive forces capable of producing cumulative strong effects (see McNaughton, 1983a, for discussion and examples). These effects are often contingent on the frequency, intensity and timing of the interactions, on the past and present states of the system, and on their interaction with future events. In this respect, the
co-occurrence of two or more events, which by themselves may have little impact, but whose interaction is synergistic, may strongly affect the system, particularly when the probability of the events occurring is low. Overall, the consequences of these interactions are not strictly deterministic but rather the product of a series of interlinked probability functions (McNaughton, 1983a).

SOIL MOISTURE DYNAMICS

Soil moisture regimes in savannas are influenced by (i) the total amount and seasonal distribution of annual rainfall and the proportion of this that enters the soil; (ii) the water holding capacity of the soil, which is largely a function of soil texture and depth, and (iii) the amount of evapotranspiration, which is related in complex ways to climate, soil texture, soil surface characteristics, and the type of vegetation at a site.

Rainfall

Mean annual rainfall in savannas ranges from about 300 mm to more than 1600 mm and normally does not exceed potential evapotranspiration, though it may do so seasonally. Most of the rain falls during one or, in equatorial regions, two, well-defined wet seasons. The dry season, which lasts as long as 9 months in semi-arid areas and as short as 3 months in moist regions, is marked by a shortage of water for plant growth, at least in the upper 1 - 2 m of the soil profile.

The spatial and temporal distribution of rainfall is often highly variable. Rain falls mainly in the form of intense, localized thundershowers, and neighbouring areas may receive different amounts of rain on any one occasion. The timing of rainfall within a wet season also varies, giving rise to different patterns in the availability of soil moisture between years. Most importantly, there are often large year-to-year differences in rainfall at a site, particularly in the dry areas.

While the rainfall in any one year is largely unpredictable, there are suggestions of longer-term, quasi-periodic fluctuations in annual rainfall in some regions (southern Africa: Tyson and Dyer, 1978), but not in others (Serengeti: Pennycuick and Morton-Griffiths, 1976). Given the large differences in primary production that occur between years in apparent response to fluctuations in the amount and seasonal distribution of rainfall (Poupon and Bille, 1974; Rutherford, 1981; Sicot and Grouzis, 1981; Dye and Spear, 1982), the possible existence and origin of these rainfall cycles, and their implications for management, needs more investigation.
Soils

The effects of variation in rainfall are compounded by differences between soils in permeability and moisture retention properties. Savanna soils vary widely in texture, structure, profile and depth, reflecting at one scale the interaction of geology, geomorphology and climate, and at another, the influence of topography, relic features of past landforms, the kind and extent of vegetation cover, and animal activity (Young, 1976; Montgomery and Askew, 1983). On a regional scale the ancient, highly weathered soils of the moist savannas, exposed to moderate to high rainfall (600 - 1600 mm p.a.), a relatively short dry season (< 6 months) and high soil temperatures (> 18°C), can be distinguished from the younger, less weathered soils of the drier savannas which experience low and variable rainfall (300 - 700 mm p.a.), and a long dry season (6 - 10 months).

Moist savanna soils: These occur mainly on the old, extensive plateaux of the Gondwana and mid-Tertiary planation surfaces, as well as on redistributed sands situated on the periphery of these plateaux and in upland basins. Most of the soils are derived from felsic or intermediate rocks (granites, gneisses, phyllites, schists, sandstones) of the underlying Precambrian continental shields. The soils are moderately to highly weathered and leached, and are generally structureless (often massive in highly weathered, clayey profiles) to weakly structured. Well structured soils occur in less weathered profiles, particularly ones derived from basic intrusions or from limestone. Kaolinitic clays and iron and aluminium oxides are the main secondary minerals. Expanding 2:1 lattice clay minerals are uncommon.

The soils are generally sandy at the surface, becoming more clayey with depth. This contrast in texture between the topsoil and the subsoil tends to be gradual in actively weathering soils but where the soils are highly weathered it is usually abrupt, giving rise to a duplex profile. Laterite is commonly present and may form massive sheets. Uniformly textured profiles are found in sandy soils derived from the weathering of sandstones and unconsolidated sediments, and in some highly weathered soils of the rain forest-savanna transition zone. The latter soils contain large amounts of free iron oxides and 1:1 lattice clays. The clays are aggregated into relatively stable sand-sized particles that impart to the profile the consistence and drainage characteristics of more loamy soils (Young, 1976; Montgomery and Askew, 1983).
Infiltration rates are generally high in sandy soils and in clays with a well-developed crack or crumb structure. However, clays with an aggregate crumb structure are susceptible to structural collapse when exposed to raindrop impact or other forms of mechanical pressure. These break up the aggregates and reduce the size of surface pores, thereby reducing infiltration rates and increasing runoff (Bridge et al., 1983). Infiltration is also reduced, even in sandy soils, by the presence of water-repellent seals. These can be caused either by dormant blue-green algae living on the soil surface, or by the accumulation of secondary chemical compounds leached from the litter. Since these seals break down with prolonged wetting, their impact is greatest early in the wet season or after prolonged dry spells.

The upper part of the soil profile in the high rainfall savannas is at or close to field capacity for much of the wet season (Young, 1976). Excess water drains rapidly down to the subsoil which can remain moist throughout the year, depending on the amount of rainfall and percolation, profile depth, proximity to groundwater, and the rate of depletion of the accumulated water by plants. Good aeration and a low mechanical resistance to root penetration in moderate to well-structured soils enables deep-rooted woody plants to utilize this moisture, often well into the dry season and long after the water content of the upper 1 - 2 m of the profile has fallen to below wilting point.

The most extreme moisture regimes occur in soils with a strongly duplex profile or which are underlain by an indurated ironstone (laterite) layer. The internal drainage of these soils is poor and, because of the reduced effective depth of the profile, they also have a low water storage capacity. Consequently, the soils are alternately waterlogged and dry (Sarmiento and Monasterio, 1975; Tinley, 1982). However, waterlogging is not confined to such soils. Site drainage on the almost level plateaux is often poor and even sandy soils can be saturated if they occur in slight depressions.

**Dry savanna soils:** Whereas moist savannas occur on plateaux and uplands, the dry savannas occur on low altitudes plains, in broad downwarped basins, and in rift-faulted valleys, often at the extremes of the tropics. The predominantly sandy and silty soils originate mainly from unconsolidated sediments, redistributed sands, and from acid igneous and sedimentary rocks of Precambrian and later age. Clay-rich profiles are less common but, where present, they contain higher proportions of expanding 2:1 lattice clays than fine-textured soils in moist savannas (Young, 1976). Since the climate is dry, the soil profile is seldom thoroughly wetted. Weathering and leaching rates are therefore low. Where highly weathered and leached soils do occur, as in Australia, these indicate the occurrence of wetter periods in the past.
As a result of the lower weathering rates, soils formed in situ from crystalline rocks, in freely-drained sites, tend to be shallow and sandy, with little or no profile development (Young, 1976). Infiltration and percolation rates are high. This favours the conservation of rainwater since it lessens the amount of moisture that can be lost through evaporation. However, this is only effective in deep sands since most of the soils are too shallow to be able to store large amounts of water.

Clayey soils in dry savannas develop in areas underlain by base-rich rocks (basalt, shales, limestones), and in poorly drained bottomlands and depressions where clays and minerals (particularly calcium and magnesium) accumulate. Self-mulching clays (vertisols) commonly occur and are particularly widespread in Australia, India and in parts of Africa. Clays with textural B-horizons, produced by clay translocation, are also common. In these soils, often high levels of exchangeable sodium cause the dispersion of clays which then accumulate in the subsoil where they restrict internal drainage, aeration and root penetration. Subsoil drainage can also be inhibited by impermeable layers formed by the precipitation of calcium carbonate and silicates. The gradual extension of these layers towards the surface reduces the effective depth of the soil and limits its water storage potential.

Infiltration rates and permeability are considerably lower in clayey profiles. This is often compounded by the presence of algal crusts or surface seals resulting from the dispersion of clay particles by raindrop impact (Penning de Vries and Djitéye, 1982). Clayey soils therefore tend to be more arid than sandy soils under equivalent low rainfall, despite having a higher water-holding capacity. In contrast to sandy soils, much of the water entering the soil is retained close to the surface where it is susceptible to evaporation. Furthermore, at given water contents, clays have more negative soil water potentials, so that proportionately less of the water in the soil is available to plants. Soil texture therefore has opposite effects on soil moisture regimes and plant water availability in moist and arid regions. Under high rainfall, clays are the wettest soils but, where rainfall is low, they are generally the most arid (Walter, 1971). In sands, the situation is reversed.

The redistribution and concentration of water by overland flow has important local effects on soil moisture regimes. In some sites in the drier savannas, more than half the incoming rainfall can be lost as surface runoff, depending on the amount of plant cover, soil surface conditions, topography, amount and intensity of rainfall, and antecedent soil moisture conditions (Walker and Cunningham, 1976; Penning de Vries and Djitéye, 1982). A smaller percentage of
total rainfall is lost as runoff in moist savannas, though absolute amounts may be higher. Much of this runoff flows onto adjacent areas where it is absorbed. This increases the effective rainfall of these sites and creates refuges for drought-sensitive plants in years of low rainfall (Macdonald, 1978). On a more local scale, termite mounds may have the same effect.

The influence of topography on soil properties and soil moisture regimes is best reflected in the regular sequence of different soil profiles which develop along a gradient from hilltop or interfluve crest to adjacent valley bottom. These soil catenas are particularly well developed in ancient, gently undulating savanna landscapes with diffuse drainage systems (Milne, 1935; Young, 1976). The changes in soil properties are related primarily to differences down the slope in (i) the extent of erosion by surface wash, associated with changes in slope angle and the distance of overland flow; (ii) the degree of leaching, downslope transport and deposition of clays and dissolved solutes; and (iii) proximity to groundwater and its seasonal fluctuations (Young, 1976). The result is the formation of well-drained and often highly-leached soils in the upper parts of the catena, and base-rich gleys in the poorly-drained, more restricted bottomlands. The changes in soil properties and moisture regimes in turn give rise to zonal patterns in the composition, structure, productivity and quality of the vegetation, and in the corresponding patterns of herbivory (Morison et al., 1948; Menaut and César, 1979; Bell, 1981; Tinley, 1982).

SOIL NUTRIENT DYNAMICS

Savanna nutrient dynamics are the outcome over a variety of time and spatial scales of interactions between climate, geology, geomorphology and the biota. Variations in the physical and chemical properties of savanna soils are strongly related to differences in bedrock and the degree to which this has been exposed by weathering and erosion. These properties have been subsequently modified by interactions between the soil, climate and geomorphology affecting soil microclimate, secondary mineral formation, and the erosion, leaching and relocation of soil and nutrients. Soil moisture and temperature in turn influence weathering and leaching rates and the level of biotic activity, particularly in the soil.

Soils

Dystrophic savanna soils: Soils derived from the weathering of acid crystalline rocks of the Precambrian continental shields, as well as those formed from ancient sedimentary formations and redistributed sands, generally have a low reserve of weatherable minerals. They are most widespread in, but are not confined to areas receiving high
rainfall and so are often highly weathered and leached. The predominance of non-expanding 1:1 lattice clays and iron and aluminium oxides results in low effective cation exchange capacity and small amounts of total exchangeable bases, particularly Ca and Mg (Jones and Wild, 1975; Lopes and Cox, 1977; Mott et al., 1985). The levels of available P are also frequently very low and some soils with an abundance of sesquioxides have a high capacity for fixing phosphorus. Except in very acid soils, the amount of organic matter is the main determinant of cation exchange capacity. The quantity of soil organic matter is positively correlated with mean annual rainfall and the length of the wet season but, overall, levels are generally low (Jones and Wild, 1975; Lopes and Cox, 1977; Kadeba, 1978; Montgomery and Askew, 1983; Mott et al., 1985).

Some highly weathered soils, particularly in South America, have high levels of exchangeable aluminium (Lopes and Cox, 1977). These pose problems for crops and introduced pasture grasses. Indigenous species, however, appear to be adapted to these high levels and some woody species accumulate the metal in their tissues (Haridasan, 1982). Outside South America, little is known about the impact of aluminium on nutrient uptake and cycling. This is a topic which needs investigation.

Eutrophic savanna soils: These soils occur in areas underlain by basic rocks and ultrabasic intrusions; in incised valleys where less weathered material is being exhumed; in alluvial deposits along drainage lines, valley bottoms or floodplains; and in areas covered by basic volcanic ash. These soils are more prominent in drier areas where the amount of rainfall has been insufficient to promote either extensive weathering or leaching. Consequently, there are usually adequate reserves of weatherable minerals (Young, 1976). The soils are less acid and may even be moderately alkaline. The often high proportions of 2:1 lattice clays, particularly in vertisols, contribute to high cation exchange capacities and higher levels of exchangeable bases. The amount of soil organic matter is generally low and therefore has little effect on the cation exchange capacity of the soil.

Organic matter dynamics

The breakdown of organic matter and the subsequent release of nutrients, as well as the roles played in these processes by the biota, differ considerably in relation to soil moisture regimes and soil fertility (Menaut et al., 1985). In the dry savannas, primary production is limited by the low rainfall and short wet season. The input of organic matter to the soil is therefore also low and highly seasonal. The quality of these inputs is generally high and much of the material is readily decomposed by the soil biota. However,
nutrient release is intermittent because microbial activity is strongly limited for much of the time by the aridity of the soil. There is a net mineralization of nitrogen at the start of the rains, though this is not sustained because the small organic matter stock is rapidly decomposed and an increasing amount of nitrogen is immobilized in the microbial biomass (Bernhard-Reversat, 1982; Penning de Vries and Djitye, 1982; Menaut et al., 1985).

In contrast, in the moist savannas, the higher rainfall and extended wet season favour high plant production and organic matter input to the soil, although this input may be limited by frequent fires. The soil microclimate favours microbial activity and there is a considerable potential for mineralization. However, microbial activity is limited by the low quality of the organic matter, principally the low levels of assimilable carbon, high C:N ratios and lignin contents and, in some cases, high amounts of condensed tannins and other secondary chemicals. The release of nutrients is slow and results in a low standing stock of available nutrients. Because of the high rainfall, the nutrients are susceptible to leaching.

Microbial activity is stimulated by exudates from plant roots and by water soluble carbon compounds which are introduced into the soil during its passage through the guts of earthworms (Lavelle et al., 1983; Menaut et al., 1985). These compounds are produced in inverse proportion to their levels in the soil, resulting in considerable biological regulation of organic matter decomposition. Because the availability of assimilable carbon is largely confined to earthworm casts and the neighbourhood of roots, the release of nutrients is highly localized.

Savanna plants maintain high root:shoot ratios. The turnover of roots, which is related to the level of plant production, may be responsible for most of the organic matter in savanna soils, particularly in frequently burned savannas where fire destroys much of the litter (Sanford, 1982). Since soil organic matter is important in maintaining soil structure and fertility, more information is needed on the sources, quality and rate of decomposition of organic material, and the factors affecting these.

Although the levels of plant-available nutrients in savanna soils are relatively low, the greater proportion of the total nutrient pool lies in the soil and soil organic matter rather than in the vegetation and litter (Nye and Greenland, 1961; Abbadie, 1983; Sarmiento, 1984; Frost, 1985). In the drier savannas, this largely reflects the relatively low plant biomass and the constraint imposed by the seasonal shortage of water on plant growth and nutrient uptake. In the more moist savannas it reflects the slow rate of release of nutrients from soil organic matter.
The rate at which nutrients cycle through savanna vegetation is relatively rapid, particularly through the herbaceous layer where nutrients turnover 2 - 4 times faster than through woody plants (Frost, 1985). The difference in the rates of nutrient turnover in woody plants and grasses extends also to litter decomposition. Grass litter, in the absence of fire and under the same conditions, decomposes 2-7 times faster than woody leaf litter, and many times faster than wood itself (Morris et al., 1982; Mott et al., 1985). Where annual fires occur, much of the grass and some of the woody litter gets burnt rather than decomposed (Hopkins, 1966; Sanford, 1982; Frost, 1985). This tends to reduce but does not entirely eliminate the difference in rates since most of the grass material that is burnt would normally decompose within a year, while woody litter takes much longer.

FIRE AND HERBIVORY

Whereas water and nutrient availability vary continuously through time within limits set by the prevailing climate, soil, and associated biological processes, fire and herbivory are events occurring at particular times, with specific intensities, at discrete intervals. These features are interrelated and, taken together, make up the particular fire or herbivory regime at a site. Since these regimes can be manipulated directly, they are potentially important management tools. However, the consequences are not always easy to predict because fire and herbivory interact, and the outcome is often contingent on the particular times, intensities and frequency of the interactions. External, unpredictable factors, such as future rainfall or drought, can also intervene and influence the outcome.

Fires and herbivores both consume and damage plant matter and are able to kill individual plants, particularly seedlings. This reduces the existing density and structure of a plant community and affects its future composition and dynamics. Although changes in plant community composition can result from pressures exerted by fire or herbivory alone, major changes usually result from their interaction. Both have relatively selective effects. Herbivory is usually limited to particular plant species and plant parts, especially those of above-average nutritional quality. Moreover, herbivore impacts tend to be restricted in space but are more uniformly distributed in time. In contrast, fire is a periodic event, often occurring over a wide area and affecting both living and dead material largely irrespective of their nutritional quality. However, fire is selective to the degree that there are considerable differences between species in their susceptibilities and responses to fire (Frost, 1984).
Fire

Most savanna fires occur during the dry season as surface fires, burning through the herbaceous vegetation. Their incidence and intensity depends on (i) the presence of sufficient fuel to support a fire; (ii) the moisture content of the fuel; and (iii) a source of ignition. Many of them are ignited by man, though in the early wet season lightning can be important. In moist savannas, fires generally occur every 1 - 3 years, but as mean annual rainfall declines, the interval between successive fires increases and becomes more variable.

The incidence of fire is largely a function of the dry-season standing crop of grass, itself a product both of the amount of rainfall and plant production during the previous wet season and the extent of herbivory. Fire intensity is variable and depends largely on the amount and structure of the fuel, its degree of curing, and prevailing ambient conditions. Because of their higher fuel load, fires in moist savannas are usually more intense than those occurring in the dry savannas.

Annual burning has little direct effect on the soil. Most effects are indirect, resulting from changes to the vegetation, and are confined to the surface soil (Sanford, 1982). Organic matter and total nitrogen are reduced and available phosphorus is slightly increased in areas exposed to regular, intense, late dry season fires. Early or less intense burns have much less of an effect (Harrington and Ross, 1974; Brookman-Amissah et al., 1980).

Burning may speed up the rate of nutrient cycling by reducing litter, especially components such as woody leaf litter and dead wood which decompose slowly. Nitrogen, carbon and sulphur are lost through volatilization and removal in smoke and ash. However, the overall significance of these losses has not been assessed. By reducing litter and herbaceous plant cover, fire also bares the soil surface, exposing it to raindrop impact, wind and sun. The length of time that the soil remains bare is variable and depends largely on the time of the fire, the rate of regrowth of the vegetation and the timing of subsequent rainfall.

Fire kills seedlings, saplings and small trees, particularly in higher rainfall areas where grass production is substantial and the annual dry-season fires are intense. Under these conditions, woody plant recruitment is generally episodic. Fire also damages aboveground parts of plants and retards the growth of shrubs and saplings, thereby lowering the biomass of woody plants (Rutherford, 1981). The effects on density are variable and depend on the rates of mortality and coppicing. Many of these effects are a function of fire intensity. The hottest fires usually occur during the late dry-
season and these can reduce a woodland canopy to coppice. Woodland species, though, are able to regenerate under a regime of less intense, early dry-season fires (Trapnell, 1959; Brookman-Amissah et al., 1980; Sanford, 1982; Edroma, 1984).

Protection from fires results in an increase in tree density and a decrease in grass production. In mesic areas, savanna woodland eventually develops but in the high rainfall savanna/forest transition zone, forest species gradually establish (Trapnell, 1959; Menaut, 1977; Brookman-Amissah et al., 1980; San José and Farinas, 1983). In the dry savannas, fires seldom occur frequently enough to limit the density of woody plants, though when they do occur, often after prolonged periods of above-average rainfall, mature woody plants may experience considerable mortality since they are more susceptible to fire than moist savanna plants.

Young trees grow rapidly in areas protected from both fire and herbivory, more so than in areas protected from fire alone. Growth in plants exposed to both pressures is severely restricted (Harrington and Ross, 1974; Belsky, 1984). Fire and herbivory therefore interact, with frequent fires keeping woody plants at a height and in an acceptable state for browsers, while the effect of the browsers is to reduce woody plant growth and keep plants within the size range affected by fire (Trollope, 1974; Pellew, 1983).

Herbivory

Savannas make up most of the world's tropical grazing lands and currently support a large biomass of domestic livestock, mainly cattle, goats and sheep. In many regions, the biomass of these species currently equals or exceeds that of the indigenous herbivores which used to occur (Cumming, 1982; Mott et al., 1985). Each of the main savanna regions in the past had a distinctive large herbivore fauna, though that of Africa appears to have been, and still is, the most abundant and diverse.

For biogeographic reasons, Australia never had any proboscids, artiodactyls or perissodactyls. Instead, these savannas were populated mainly by macropods (kangaroos and wallabies), some of which survive today alongside feral and domestic ungulates. South America, in contrast, had a diverse fauna of large ungulate and non-ungulate herbivores throughout the Tertiary, with most of the species becoming extinct during the late Pleistocene either as a result of concurrent climatic change or the arrival of man (Martin and Wright, 1967). What proportion of these species actually inhabited savannas is not known, but the present-day indigenous fauna and the carrying capacity for domestic livestock on natural rangeland is relatively low.
Only Africa, and to a lesser extent India, currently have significant populations of indigenous ungulates and other large herbivores. West African savannas support lower numbers and a smaller biomass of large herbivores than do those in eastern, central and southern Africa (Bell, 1982; Milligan et al., 1982). This partly reflects the high hunting pressure and partly the impoverished soils, low quality vegetation and consequent low carrying capacity of the West African savannas.

Studies of herbivory in savannas have focussed largely on the effects of wild large ungulates, mainly in African ecosystems. It must be emphasized however that these are not the only nor necessarily the most important herbivores in savannas. In many areas today, domestic livestock, especially cattle, have effects that override those of indigenous species. Moreover, harvester termites, leaf-cutting ants, lepidoptera larvae, and grasshoppers (particularly locusts), all have major effects in some systems, though in most cases these have not been quantified.

There is considerable variation among herbivores in the degree of selectivity in their diets, reflecting a complex interplay between the kind of animal, its body size and associated energy and nutrient requirements, and the growth form, structure, chemistry and phenology of potential food plants. The functional responses of herbivores to changes in plant abundance are also important, though these have not been sufficiently studied.

Vertebrate and invertebrate herbivores in savannas both show a marked preference for feeding either on broadleafed, often woody plants, or on grasses and sedges. Mixed feeders are much less common. This specialization reflects the very different nutritional and other features of these plant groups. Crude protein levels in woody plants are generally higher than in grasses, but the digestibility of plant tissue is reduced by high levels of structural carbohydrates and, in some instances, by secondary chemical compounds such as condensed tannins (Cooper and Owen-Smith, 1985). Thus browsers tend to be energy-limited whereas grazers are often protein-limited. Moreover, browsers can experience severe food shortages during the dry season when woody plants drop their leaves.

The effects of herbivory depend on (i) the growth form of the plant; (ii) the plant parts removed; (iii) the intensity, frequency and season of use; (iv) the growth stage of the plant; (v) soil type and soil moisture conditions, which affect water and nutrient availability and thereby the plants capacity to regrow; and (vi) the history of the plant, particularly the time since a previous occurrence of defoliation by other herbivores or fire. Since recovery from defoliation is not instantaneous, future events such as heavy rainfall, drought, or further defoliation by herbivores and fire can also influence the eventual outcome.
Compensatory growth is one of the main responses of plants to defoliation. When defoliation is low, plants just compensate by replacing lost tissue. Under moderate levels of defoliation, and provided that moisture and nutrient conditions for growth are adequate, some plants overcompensate for amounts removed, leading to an increase in aboveground plant production (McNaughton, 1985). If a plant is severely defoliated, the amount of regrowth is insufficient to compensate for the amounts of foliage removed, in which case continued defoliation would eventually result in the plant being killed or so reduced in size and stature that it is ultimately overlooked by herbivores.

Consumption by herbivores accelerates the processes of energy flow and nutrient cycling. Defoliation reduces nutrient and water limitations on the remaining tissues and stimulates growth. In some cases, photosynthetic and nutrient uptake rates are increased (McNaughton, 1979). By reducing a plant's transpirational area, defoliation also contributes initially to a lower level of water-use and, thereby, to the conservation of soil moisture. This can lead to an extension of the normal growing season (McNaughton, 1985).

Nutrients that would otherwise be bound up into standing dead plant matter and litter are recycled more rapidly. Furthermore, by recycling nutrients in concentrated form as dung or urine, herbivores contribute to maintaining a high availability of nutrients for plants. Where the potential for leaching from the soil is high, this serves to keep the nutrients cycling rapidly through the vegetation and surface soil, a feature which may be crucial to maintaining the longterm nutrient status of these systems (Botkin et al., 1981).

Herbivory interacts with fire in both space and time. Many grazers are attracted to recently burnt ground to feed on the post-fire regrowth of grasses (Frost, 1984). This stimulation of regrowth at a time of the year when the plants are usually dormant, together with the higher nutritional quality of the regrowth, is a major reason for the frequent ignition of dry-season fires by pastoralists in tropical savannas (Medina pers. comm., Milligan and Sule, 1982). Grazers in turn reduce grass biomass and so lower the short-term probability of the area sustaining another burn. Patchy grazing consequently causes patchy fires and visa versa.

For browsers, dry season fires can reduce the availability of food and cause the animals to disperse to other, unburnt, areas (Bell and Jachmann, 1984). This may increase the browsing pressure on trees in these areas (Harrington and Ross, 1974). The degree of concentration or dispersion, and subsequent effects such as overuse and trampling, depend on the size of the burnt patch in relation to the amount of unburnt vegetation, and their relative attractiveness to herbivores.
INTERACTIONS

Effects of vegetation on water and nutrient dynamics

The relationship between soils and vegetation is interactive: the nature of the soil greatly influences the type of vegetation that occurs at a site, while the vegetation affects soil properties both directly, through the supply of organic matter, and indirectly, by affecting soil moisture and temperature regimes, soil chemistry, and the stability of the soil surface. The extent of plant and litter cover affects the flux of water between the atmosphere and the soil by intercepting and redistributing rainfall, enhancing infiltration rates and lowering the rate of evaporation of water from the soil surface (Kelly and Walker, 1976).

At the same time, plants deplete the soil moisture store by taking up and transpiring water. The rate of water loss depends partly on soil water potentials, partly on the evaporative demand of the atmosphere, and partly on plant characteristics such as total leaf area, plant water potentials, transpiration rates and stomatal responses to increasing water deficits.

There are few data available on the transpiration rates of savanna trees and grasses. In moist South American savannas, where trees have access to water throughout the year (Sarmiento et al., 1985), the trees have only marginally lower transpiration rates than grasses (Goldstein, pers. comm.). Therefore, the relative rates at which trees and grasses deplete the soil water in such a system will depend largely on the relative leaf areas of the two components.

In the dry savannas, where both trees and grasses experience a seasonal water deficit, there appears to be a difference in their responses to increasing water stress (Walter, 1971; Pendle, 1982). In grasses, transpiration rates appear to be regulated primarily by atmospheric evaporative demand. By making osmotic adjustments to leaf water potentials through concentrating solutes in their leaves (Wilson et al., 1980), grasses seem able to maintain relatively high rates even at soil moisture levels near wilting point. While this extends the period of physiological activity of the grasses, it results in a rapid depletion of soil moisture in the rooting zone of grasses and this eventually leads to large leaf-water deficits, desiccation and, often, leaf death.

In contrast, the transpiration rates of trees in the dry savannas appear to be determined more by soil moisture availability than by atmospheric demand. As the soil dries out, the trees regulate their
water-use by lowering transpiration rates through stomatal closure, or by reducing leaf area through shedding leaves. Trees therefore deplete the soil moisture store less rapidly and completely than do the grasses. The result is that where rainfall is low and grasses predominate, the vegetation aggravates the shortage of water by extracting moisture from below the zone in the soil where it can be removed by evaporation alone. This heightens the contrast between the wet and dry phases of the soil. On the other hand, where rainfall is high and tree growth is favoured, soil moisture tends to be conserved.

Trees also influence the status and distribution of nutrients in savanna soils. Woodland regeneration, following protection against sustained heavy browsing and grazing, results in an improvement in soil nutrient status (Hatton and Smart, 1984). Soil organic matter, pH, available phosphorus, and the level of exchangeable cations (excepting Mn) all increase. This is because trees, with their relatively deep root systems, are able to extract nutrients at depth in the soil and so counter the effects of leaching (Kellman, 1979).

The horizontally-extensive root systems of trees allow them to concentrate nutrients from a wide area (Van Donselaar-Ten Bokkel Huinink, 1966; Radwanski and Wickens 1967; Foldats and Rutkis, 1975). Consequently, the soils under trees in savannas generally have a higher nutrient status which, together with the moister soils and more mesic microclimate, influences the distribution of herbaceous plants, favouring more mesic-adapted, palatable grasses. This occurs in both Africa and Venezuela (Kennard and Walker, 1973; Medina, pers. comm.) but not in northern Australia (Mott et al., 1985) which poses an interesting question why.

Effects of animals on water and nutrient dynamics

Animals affect the structure of the soil and therefore soil moisture dynamics in various ways. Soil macrofauna incorporate litter and other organic materials into the soil and contribute to the synthesis of organic colloids. These colloids are involved in the formation of stable soil aggregates which in turn enhance the aeration, permeability and water-holding capacity of the soil. The network of underground galleries and burrows formed by soil animals presumably has similar positive effects but these have not been thoroughly investigated (Woods and Sand, 1977). Earthworms and termites bring considerable quantities of soil to the surface in the form of faecal casts, galleries, and surface sheetings (Wood and Sand, 1977; Bagine, 1984; Lavelle, 1983). This improves soil surface structure, thereby promoting high water infiltration rates.
Much of the material brought to the surface by termites and earthworms comes from the subsoil. This counteracts the effects of illuviation and leaching, and so contributes to the maintenance of uniform-textured soil profiles (Boyer, 1973; Young, 1976; Josens, 1983; Lavelle, 1983). Termites are particularly important in this regard as they generally select clay-sized particles in preference to sand when constructing their nests and galleries (Wood and Sands, 1977). This can have both positive and negative effects on the soil moisture balance, depending on rainfall.

Direct negative effects of animals on soil moisture regimes result from compaction of the surface soil and the breakdown of aggregates through trampling. This increases bulk soil density, reduces infiltration rates and lowers the water-holding capacity of the soil. Run-off and erosion increase. Indirect negative effects are mediated through the impact of animals on the vegetation. High densities of large ungulates and invertebrate herbivores such as harvester termites significantly reduce plant and litter cover (Kelly and Walker, 1976; Lepage, 1981). This increases the exposure of the soil surface to raindrop impact, sun and wind, and leads to more extreme soil surface temperatures, higher evaporation rates and, ultimately, to the structural collapse and deflation of the soil surface. Impermeable surface seals are often formed, resulting in a cycle of degradation of reduced infiltration rates, increased run-off, lower seedling establishment, less plant production and further exposure of the soil surface (Kelly and Walker, 1976; Macdonald, 1978; Bridges et al., 1983; Valentin, 1985).

Local differences in soil type and organic matter production result in considerable small scale variations in soil nutrient status. These differences are heightened by the activities of termites. Litter feeding termites are particularly common in dystrophic savannas where they may consume up to 36% of annual litterfall, including about 60% of dead wood and grass litter production (Wood and Sands, 1977; Ohiagu, 1979b; Josens, 1983). Thus considerable amounts of organic matter and nutrients are concentrated in termite nests, from where they are slowly released into the soil as the mounds weather. There have been relatively few studies of the turnover times of termite mounds. The turnover of *T. erminatus* mounds in a Nigerian savanna averages 6.3 years (Ohiagu, 1979a) but in other species the turnover times are much longer. The amount of organic matter and nutrients added to the soil each year is generally low (Wood and Sands, 1977). Therefore, while the concentration in, and subsequent slow release of material from termite mounds may conserve organic matter and secure nutrients against leaching (Menaut et al., 1985), it may equally limit the cycling of nutrients in savannas.
Soil moisture and the tree: grass equilibrium

Differences in soil moisture regimes and in the relative availability of moisture and nutrients to plants are major factors determining the wide variation in the structure of savanna vegetation. Savannas encompass a range of physiognomic types, from grassy shrublands at the interface with deserts, through open woodlands and treeless edaphic grasslands, to almost closed woodlands with a heliophytic grass understory in the transition zone to semi-deciduous and evergreen forests (Huntley and Walker, 1982). The characteristic feature serving to link this diversity of vegetation types is the normally stable coexistence of grasses and trees, components which in the other major biomes tend to replace one another.

To account for the balance between woody plants and grasses in the dry savannas, Walter (1971) suggested that the soil consists of two functionally distinct layers: a surface layer in which grasses, with their shallow compact root systems, retain and have prior access to the water entering the soil; and a lower subsoil layer to which the deeper-rooted woody plants have exclusive access. In terms of this hypothesis, trees and grasses can coexist in situations where the amount of water regularly reaching the subsoil is just enough to support trees but insufficient to enable them to establish a continuous canopy and shade out the grasses. The hypothesis has been formalized by Walker et al. (1981) and Walker and Noy-Meir (1982).

The limited information available on the root systems of savanna plants indicates that there is considerable vertical overlap between grass and tree roots, though the maximum density of grass roots occurs in the top 10 - 20 cm of the soil, while in trees it is generally below this (Strang, 1969; Rutherford, 1983; Knoop and Walker, 1985). However, both have access to surface and subsoil water (Russell, 1966; Strang, 1969; Tunstall and Walker, 1975; Knoop and Walker, 1985). Despite this weakness in one of the major assumptions of the model, it can still be valid provided that the grasses and trees are each the superior competitor in different parts of the soil profile or at different times (Knoop and Walker, 1985).

The higher transpiration rates and more compact root systems of grasses should give them an advantage in the upper layers of the soil. On the other hand, once trees are established, they can outcompete grasses by shading them and, through being longer-lived, by gradually appropriating space in the soil when it becomes available. The lower rates of water-use of trees in the dry savannas are also an advantage since the available soil moisture in those parts of the soil profile dominated by tree roots will not be depleted so rapidly. This enables trees to remain active for longer.
Subsoil moisture levels are determined mainly by the amount of water draining through from the surface. The relative abundance of grass and trees will therefore depend on both the amount of rainfall and the water-holding capacity of the topsoil. In areas of low rainfall, particularly where the water-holding capacity of the topsoil is high, most of the incoming water remains near the surface. This allows grasses to reduce the amount of water eventually reaching the subsoil, thereby limiting indirectly the growth of trees (Knoop and Walker, 1985). Since there is a shortage of available moisture, neighbouring trees are potential competitors. This is sometimes reflected in the regularity of their spatial distributions (Smith and Walker, 1983).

Trees are increasingly favoured as more water reaches the subsoil. This generally occurs on deep, porous sands, stony slopes, fractured lateritic outcrops and on well-drained soils in regions with high annual rainfall (Walter, 1971; Walker and Noy-Meir, 1982; Knoop and Walker, 1985). As tree densities increase, grass growth declines both through shading and through increased competition for water and nutrients. Tree removal results in increased grass production (Beale, 1973; Walker et al., 1972; Dye and Spear, 1982), though total aboveground plant production usually declines. In most cases, grass production is highest where woody plants have been completely cleared, but in some cases it reaches a maximum in lightly wooded communities (Kennard and Walker, 1973). The increase in grass production is often accompanied by a change in grass species composition and a reduction in the abundance of better-quality grasses (Dye and Spear, 1982).

While competition for water may explain the coexistence of grasses and trees in the dry savannas, it does not adequately account for the presence of savanna vegetation under much higher rainfall. In the moist South American savannas, for example, the dominant trees are largely evergreen, deep-rooted and do not markedly reduce their transpiration rates during the dry season (Rawitscher, 1948; Vareschi, 1960; Foldats and Rutkis, 1975; Sarmiento et al., 1985). Most of the species renew their leaves in the middle of the dry season when conditions seem least favourable for leaf expansion (Medina, 1982; Sarmiento, 1984). For the trees to remain physiologically active at this time, they must have access to adequate moisture, either from groundwater sources or from moisture which has accumulated deep in the soil profile during the previous wet season (Foldats and Rutkis, 1975; Sarmiento, 1984).

A shortage of water is therefore unlikely to be the main factor limiting tree densities in these savannas. Soil nutrient levels though are extremely low (Lopes and Cox, 1977; Sarmiento, 1984). This is manifested in the slow growth and scleromorphism of the
woody vegetation which, together with the large investment made by these plants in their root systems, limits the rate of development of a closed tree canopy. Grasses can therefore coexist alongside the trees despite being dormant for most of the dry season. Moreover, because they are shallow-rooted and relatively fast growing, the grasses are able to take up nutrients rapidly when these are mineralized in the surface soil during the wet season. This probably further limits the availability of nutrients to trees.

Fire may also be a factor since it limits the establishment of trees and shrubs and retards the development of a closed canopy, enabling grasses to coexist alongside trees. Plants on infertile soils are particularly prone to fire. The slowness with which closed tree and shrub canopies develop enables the grasses, which fuel the fires, to persist under trees for longer (Kellman, 1984). Most of the fires occur during the dry season when the grasses and other herbaceous plants are dormant and therefore relatively unaffected by fire.

In contrast, most woody plants, even those species which tend to be fire-tolerant as adults, are sensitive to being burnt during the early stages of establishment and growth, particularly by intense late dry-season fires (Silva and Castro, 1985). The biomass of established woody plants is also reduced as fire damages the aboveground parts and retards their growth. Fire, therefore, favours grass production and this, in turn, fuels future fires, thereby setting up a positive feedback which maintains both grass and fire in the system. Under conditions favouring rapid and substantial grass growth, fires may even be sufficiently intense to maintain an open grassland.

Not all grasslands in the high rainfall savannas owe their origin to regular fires. Pure grasslands also occur wherever there is poor site drainage and/or where a shallow soil profile overlies an impermeable clay horizon or laterite layer (Michelmore, 1939; Sarmiento and Monasterio, 1975; Tinley, 1982). The moisture regime of these soils fluctuates between an excess of water during the rains and extreme water deficit in the dry season. This does not affect shallow-rooted grasses and sedges but is inimical to the growth of the deeper-rooted trees. In some areas, such as the llanos of central Venezuela, the scattered occurrence of trees reflects local differences in soil depth and the structure of the underlying laterite layer. The trees occur where the soil is sufficiently deep and porous so that waterlogging doesn't occur, or where their roots are able to penetrate cracks in the laterite and thereby gain access to groundwater during the dry season (Monasterio and Sarmiento, 1968; San José and Farinas, 1983). Competition between trees and grasses is not a factor in this case.
Changes in the abundance of trees and grasses at a site imply differential mortality or survival of individuals of different species. Water stress, fire and herbivory appear to be the main causes of seedling mortality (Silva, 1973; Penning de Vries and Djitbye, 1982; Belsky, 1984). Little is known about the processes of seed germination and seedling establishment in savannas, or about the role of competition, particularly from established plants. Both grasses and trees can inhibit the establishment of woody plant seedlings, but the precise mechanisms are not known (Strang, 1969; Knoop and Walker, 1985). Competition for water and nutrients may be indirectly involved. Since smaller seedlings are generally the most susceptible to water stress, or to being burnt or eaten, any limitations on growth will increase the risk of mortality. It is therefore important to learn what factors favour the recruitment of new individuals to a population. Does an increase in percolation favour an increase in seed production of adult plants, or does it result in improved seedling growth and survival? Studies of the population biology of selected tree and grass species will be essential in order to understand the mechanisms involved.

Species composition and coexistence

In savannas there is generally an inverse relationship between plant species richness and the moisture and nutrient status of the soil. Well drained, sandy dystrophic soils can have up to twice the number of species coexisting at a site compared with sites on eutrophic, poorly drained clays (Frost, pers. comm.). The underlying mechanisms giving rise to this relationship have not been investigated. Two, not mutually exclusive explanations seem plausible. First, low nutrient availability restricts plant growth and reproduction with the result that the rate at which populations approach competitive equilibrium is reduced. This may limit the dominance of certain species and enable a greater number of potential competitors to coexist. In variable environments such as savannas, this coexistence may be prolonged indefinitely if the competitiveness of different species alternates with the changes in the environment. In this respect, it is worth noting that while the diversity of species on clayey soils is often low, the changes in composition are more marked, reflecting the greater amplitude of change in conditions on clays per unit change in rainfall (O'Connor, 1985).

Secondly, if nutrient limitation is of prime importance to plants growing on dystrophic soils, then selection should favour attributes which enhance a plant's capacity to take up and store nutrients. These may involve specialization on a narrow array of microsites with particular soil characteristics and nutrient status. Where there is considerable heterogeneity in the soil, this would provide more opportunities for coexistence and, thereby, a higher diversity.
The spatial heterogeneity of savanna soils is marked. Features such as termittaria, large mammal activity sites (dung sites, burrows etc.), the patchy occurrence of fire and grazing, and inherent discontinuities in the vegetation (bushclumps, open and under-tree sites), all contribute to differences in soil characteristics. Marked differences in species composition and abundance can readily be observed over short distances in relation to this heterogeneity, suggesting that optimal sites for different species are generally limited to one or a few sites along an edaphic gradient. At the same time, since establishment appears to be a critical stage for many plants, some of these differences may reflect processes operating primarily at the seedling stage.

The marked effect that changes in soil chemistry have on grass species composition is clearly indicated by the changes which occur in response to fertilization (Mills, 1964; O'Connor, 1985). The extent of these changes depends both on soil type, being more pronounced on dystrophic sands than on eutrophic clays, and on rainfall, being more apparent in the wetter savannas, paralleling the observed differences in species richness.

There are also wide differences in the moisture requirements of savanna plants. This is reflected in the differential distribution of species along soil moisture gradients (Silva and Sarmiento, 1976; Yeaton et al., in prep.); in differences in water-use by species growing under the same climatic conditions (Foldats and Rutkis, 1975; Medina, 1982); and by short-term changes in both woody and herbaceous community composition occurring during periods of above- and below-average rainfall (Poupon, 1979; Singh and Krishnamurthy, 1981; O'Connor, 1985). These changes in species composition are usually greater on clayey than on sandy soils, reflecting the more extreme soil moisture regimes of clays.

The composition of the herbaceous layer in dry savannas appears to be affected primarily by year to year and longer-term variations in rainfall. The effects of grazing or fire become more important as mean annual rainfall increases and its variability declines. For example, in the Australian moist tropical and subtropical tallgrass savannas, introduced ungulates (cattle and sheep) and increased fire frequencies have apparently caused a change from a Themeda australis dominant understory to one dominated by Heteropogon contortus (Shaw and Bisset, 1955).

**Phenology and coexistence**

Seasonal variations in water and nutrient availability, together with competition from other plants, and stresses imposed by the annual dry season, fire and herbivory, create a spatially and temporally shifting mosaic of challenges and opportunities, which is
reflected in the wide variety of phenological behaviour found among savanna plants. As many as 15 functionally distinct phenological groups have been recognized, based on the seasonality/aseasonality of carbon assimilation, continuous versus periodic shoot growth, and the time of flowering (Sarmiento and Monasterio, 1983).

Herbaceous plants have the widest variety of phenological responses (Menaut and César, 1979; Sarmiento and Monasterio, 1983; Singh et al., 1985). Most species are perennial, becoming dormant or semi-dormant during the dry season. Growth during the wet season is rapid, particularly among grasses. Flowering and seed set usually take place later in the wet season but there are wide differences between species in this respect (Menaut and César, 1979; Singh et al., 1985). Some species flower in response to early rains, others in response to late rains. Many of the perennial forbs flower towards the end of the dry season or at beginning of the rains. Flowering and seed dispersal in some of these species is initiated by fire (Coutinho, 1982; Menaut and César, 1979). Most species, though, reproduce on a fixed schedule, irrespective of when the rain falls or fires burn. A few species grow continuously; others are opportunists, growing whenever conditions are favourable.

A large number of annuals occur in some savannas. These species differ widely in their timing and rate of development, and include some species which are capable of completing their life cycles rapidly and opportunistically whenever conditions are suitable (van Donselaar-Ten Bokkel Huinink, 1966; Menaut and César, 1979; Sarmiento, 1984). In arid savannas, the differences in germination time reflect responses to two opposing selection pressures: the advantage of rapid germination enabling individuals to exploit fully the brief flush of water and nutrients at the start of the short growing season, and the risk that subsequent rains will fail and that the plants will become dessicated before they can reproduce (Penning de Vries and Ojitéye, 1982). Given the inherent variability of savanna environments, particularly the stochastic nature of the rainfall, the diversity in phenology found among herbaceous savanna plants is probably a key feature promoting their coexistence.

The phenology of woody plants is much less variable. Most of the species in African, Australian and Indian savannas are deciduous (Malaisse, 1974; Menaut, 1983; Sarmiento and Monasterio, 1983; Mott et al., 1985). They shed their leaves during the dry season, remain leafless for a few weeks to months, then produce new leaves prior to or at the beginning of the following wet season. The time of leaf fall appears to be related to water stress, the trees retaining their leaves for longer in years of high rainfall. Some species are only briefly deciduous, the old leaves falling just before the new ones emerge at the start of the annual rains. Leaf-out in deciduous species coincides with an increase in both mean daily temperature and photoperiod (Rutherford and Panagos, 1982).
Leaf production in the deciduous species of the moist savannas is largely deterministic. This and annual shoot growth are apparently derived from carbohydrate and nutrient reserves stored in the plant. The greater part of the wet season is devoted to photosynthate production and the replenishment of these reserves, as well as to radial growth and root extension (Rutherford and Panagos, 1982). In contrast, in the drier savannas, shoot growth is indeterminate and depends on conditions during the current growing season.

Evergreen savanna trees and shrubs are only common in the high rainfall savannas of South America. These species, which are deep rooted and generally appear to have access to an adequate water supply, replace their foliage during the middle of the dry season. This facilitates the nutrient economy of these trees in two ways. First, it enables nutrients to be withdrawn from senescing leaves and to be reallocated immediately to the newly developing leaves. Secondly, because the expansion of the new leaves, which are highly leachable, takes place during the dry season, the risk of nutrient loss through leaching is reduced (Sarmiento et al., 1985).

Flowering and fruiting are also strongly seasonal. In Australian and South American savannas, flowering occurs mainly during middle of the dry season and is frequently associated with defoliation by fire or drought (Coutinho, 1982; Mott et al., 1985). Fruits mature rapidly and the seeds of most species are dispersed during the following wet season (Sarmiento, 1984). In African savannas, flowering is concentrated at the end of the dry season and beginning of the wet season, occurring at the same time as leaf-out. Fruits mature during the wet season and are dispersed throughout the following dry season (Hopkins, 1970; Malaisse, 1974; Menaut, 1983).

Plant production

Organic matter production and plant quality in savannas depend on the total amount and seasonal distribution of rainfall, and on the availability of nutrients, particularly nitrogen and phosphorus (San José and Medina, 1976; Penning de Vries and Djitły, 1982; Mott et al., 1985). The influence of water availability is most apparent in the drier savannas, as indicated by the positive correlations between annual rainfall and, for example, herbaceous aboveground biomass (Walter 1971; San José and Medina, 1976; Rutherford, 1981; Deshmukh, 1984; Singh et al., 1985). However, the relationship is only very general and is affected by factors such as the duration of the wet season, soil type and texture, nutrient availability, temperature, fire and species composition (San José and Medina, 1975; Rutherford, 1981; Penning de Vries and Djitły, 1982; Singh et al., 1985).
The different patterns of plant production on clayey and sandy soils occurring along rainfall gradients, or in response to fluctuations in annual rainfall at a site, clearly illustrates the influence of soil texture on water availability and production. When rainfall is low, production on clays may be as low as, or even lower than that on sandy soils under the same rainfall, despite the generally higher nutrient status of clays. However, production on clays increases more rapidly with increasing rainfall (Dye and Spear, 1982). The result is that, in relation to the same fluctuations in rainfall, production on clayey soils is much more variable than on sands.

As rainfall and the length of the wet season increase, water becomes less limiting and other factors, such as low nutrient availability, begin to limit production (Mott et al., 1985). For example, grasses growing on inherently fertile soils, or on ones which have been artificially fertilized, are much more productive than those growing on infertile or unfertilized sites (Mills, 1968; San José and Garcia Miragaya, 1981; Penning de Vries and Djitte, 1982). The effects are more pronounced when water is not limiting (Donaldson et al., 1984). Improved soil fertility increases the use of water by the vegetation, improves water-use efficiencies, and thus contributes to higher production. However, the available soil moisture is used up more rapidly, thereby shortening the period for active growth and increasing the risk of physiological drought.

The level of production is strongly influenced by the relative availability of nitrogen and phosphorus. Additions of nitrogen or phosphorus alone do not result in significant increases in biomass production unless the other nutrient is already present in excess. Nitrogen-fixing legumes, for example, show a positive response to the addition of phosphorus alone (Penning de Vries and Djitte, 1982). However, when nitrogen and phosphorus are added simultaneously there is a massive increase in biomass production, particularly of grasses (Norman, 1962; Medina et al., 1978; San José and Garcia Miragaya, 1981; Penning de Vries and Djitte, 1982; Mott et al., 1985).

Overall, organic matter production in savannas is limited mainly by nitrogen supply. The grasses of the humid, dystrophic savannas of South America, for example, seem to be adapted to low phosphorus availability. Fertilization experiments conducted in Australia (Norman, 1962), South Africa (Weinmann, 1938) and Venezuela (Medina et al., 1978; San José and Garcia-Miragaya, 1981) show that when nitrogen is limited, fertilization with phosphorus increases the phosphorus content of the newly produced aboveground biomass. This is not retranslocated before canopy dries at the end of the rainy season (Medina, in press).
Low nutrient availability is not confined to the wetter savannas. There is a high potential for nutrient limitation in situations where growth must be completed in a relative short period. Rapidly growing plants have a high nutrient demand and can temporarily deplete the soil of available nutrients, particularly where nutrient mineralization is intermittent. This is an important constraint in arid savannas where the growing season is short and where the stock of available nutrients is sustained by mineralization of a limited amount of soil organic matter (Penning de Vries and Djitbye, 1982). Differences in the times of peak nutrient availability add a further complication. In the Sahel, for example, nitrogen mineralization peaks at the start of the wet season when the plants are limited by a lack of phosphorus. Later, as the wet season progresses, nitrogen is increasingly immobilized by the soil biota and this eventually limits plant growth (Penning de Vries and Djitbye, 1982).

The increasing nutrient constraints faced by savanna plants through the growing season are clearly seen in the seasonal changes in plant quality (Shaw and Bisset, 1955; Afolayan and Fafunsho, 1978; Mott et al., 1981; Penning de Vries and Djitbye, 1982). Nitrogen and phosphorus contents in leaves are high at the start of the wet season and decline progressively as the plant grows. Plant quality is especially low during the dry season and this becomes an important constraint on secondary production. Average pasture quality is often below the minimum maintenance levels for domestic livestock and wild ungulates. The animals compensate for this decline to some extent by foraging selectively on those components in the herb layer which have higher than average forage quality (Bremen and de Wit, 1983). Nevertheless, they still experience a loss in decline in body condition.

Attempts to overcome these deficiencies include the use of mineral supplements (urea/molasses mixtures), crop residues, fodder reserves, and the improvement of pasture quality by introducing plant species (principally legumes) which will provide the necessary elements (Tothill et al., 1985). Supplementation generally results in heavier stocking rates, increased natural pasture utilization and reduced incidence of fire. The introduction of alien species into natural pastures requires the addition of non-nitrogenous fertilizers, usually superphosphate. This often results in higher soil fertility, improved forage quality, and increased carrying capacities for livestock. In areas with a long, harsh dry season, this can cause a breakdown in the stability of the herbaceous layer with annual grasses and weeds replacing the native perennials (Mott et al., 1981). The influence of these management actions on the longterm stability of these systems needs to be investigated.
The effect of fire on herbaceous production depends both on the time of burning and on soil moisture availability. Fire tends to increase grass production in high rainfall areas with a short dry season, but in drier areas production is generally reduced relative to neighbouring unburnt areas (West, 1965; San José and Medina, 1975). The season of burn has an important bearing on the outcome. Early dry season fires induce plants to flush at a time when soil moisture levels are already declining. This regrowth rapidly depletes the remaining soil moisture and the tillers do not survive. The potential stimulus to production is therefore not sustained. Growth at the start of the following wet season is initiated simultaneously in both burnt and unburnt plants. Burning at, or soon after the start of the first rains generally has the same outcome except where growth in unburnt plants is limited by an accumulation of standing dead matter.

In contrast, defoliation by fire during the latter part of the dry season results in equilibration of plant and soil water potentials, allowing plants to grow. Provided that the soil moisture store is replenished by early wet season rains before it is again depleted by the grasses, this early start to the growing season results in a higher production by burnt plants (San José and Medina, 1975). Depending on the amount of herbivory, the dry season standing crop of grass on regularly burnt areas can be higher than on unburnt plots. This increases the probability of fire, setting up a positive feedback loop that serves to maintain a high fire frequency and high grass production.

Plant quality

Primary production in savannas has three possible fates: it can be consumed by herbivores, it can be burnt, or it can senesce, die and decompose. The amount of plant matter incorporated directly into the litter and soil depends on the extent of both herbivory and fire. In turn, the incidence of fire is largely a function of the dry season standing crop of grass, a product of the level of production during the preceding wet season and the intensity of herbivory. The major determinant of herbivory appears to be plant quality (Bell, 1982, 1984).

Plant quality, in terms of the suitability of plant matter as food for organisms further along the food chain, can best be defined as the ratio of assimilable plant matter (mainly protein-based compounds and soluble carbohydrates) to the amounts of unusable and inhibitory material in a plant (mainly fibre, lignin and secondary chemical compounds), rather than as the absolute amount of crude protein and soluble carbohydrate present in a plant (Bell, 1981).
The availability of soil water and nutrients such as N and P influence plant quality by altering the relative production of cytoplasmic and structural components. Total biomass and protein production both increase with increasing water and nutrient availability (San José and Medina, 1976; Medina et al., 1978; Bell, 1981, 1982; Penning de Vries and Djitéye, 1982; Breman and de Wit, 1983). However, the production of carbon-based compounds such as fibre is less affected by a shortage of nutrients than is protein production, so that where nutrients are limited relative to water, plant quality is low. On the other hand, protein production is stimulated more than fibre production by an increase in the availability of nutrients. This increase may be absolute (e.g. through fertilization) or relative (e.g. through a decrease in water availability.

Plant quality, therefore, will be affected by any process which alters the relative availability of water and nutrients to plants. For instance, low rainfall, low infiltration rates caused by soil capping, low plant cover, or degradation of the soil surface by herbivore trampling, all result in low water availability. This, in turn, results in the production of a small amount of good quality plant biomass which may result in a greater proportion of the vegetation being consumed, less plant cover, more trampling and increased soil degradation. In contrast, increasing water availability results in the production of more plant biomass of increasingly poor quality (Breman and de Wit, 1983), lower animal consumption, and an increasing proportion of the available nutrients being concentrated in the plants. This leads to a lower availability of nutrients in the soil, lower plant quality and even less consumption.

Vegetation dynamics

The relationship between water and nutrient availability at different layers in the soil, competition between plants for these resources, and the resulting patterns of plant production and quality, are the key to understanding the dynamics of savanna vegetation in relation to herbivory and fire (Bell, 1981, 1982, 1984). For eastern, central and southern African savannas, four main patterns of herbivory, fire and vegetation dynamics emerge, based on the relative availability of soil moisture and soil nutrients (Bell, 1984). With the exception of the numbers and impact of large herbivore populations, which are characteristic of these savannas, the patterns appear to have counterparts in other savanna regions.

In areas of low water availability and high nutrient supply, the vegetation consists largely of high quality grasslands and open woodlands. Examples include the Serengeti and Amboseli regions of East Africa, parts of the Deccan of India and the Astrebla-dominated
grasslands on the Barkly Tablelands of Australia. In Africa these areas support a high biomass and wide diversity of indigenous large herbivores in which smaller-bodied species requiring high quality diets predominate. Where these species are now absent, there is usually an equivalent biomass of domestic livestock.

A large proportion of the annual above-ground production is consumed. For example, on the Serengeti plains, an average of 66%, and up to 94%, of net aboveground primary production is consumed annually by large herbivores alone (McNaughton, 1985). In this case, the animals are inducing substantial compensatory growth in the plants thereby creating a high nutrient demand and promoting high nutrient uptake rates (McNaughton, 1983b, 1985). Because of this compensatory growth, the energy flow to consumers is additive and can, in some cases, be maintained with little or no reduction in plant biomass (McNaughton et al., 1983).

Regular defoliation appears to be one of the main factors maintaining the high number of coexisting grass species. Changes in species composition and a decline in diversity come about when an area is protected from grazing or fire. Parallel changes, involving a different suite of species, occur in areas that are exposed to very heavy or very frequent defoliation (McNaughton, 1979, 1983a). However, this does not necessarily imply that the most diverse community is the most moderately grazed (McNaughton, 1983a), though this can happen (Singh, 1976). Overall, fire is probably less important than grazing, partly because it is a dry season phenomenon occurring at a time when the grasses are dormant, and partly because the levels of consumption are usually so high that there is insufficient grass biomass left during the dry season to fuel a fire. The incidence of fire is therefore low, other than after exceptionally wet years. Overall, these systems can be characterized as being highly variable but resilient (Norton-Griffiths 1979).

At the other extreme are systems in which water availability is high but the soils are extremely nutrient-poor. Such systems are dominated by trees and shrubs and include the miombo woodlands of the Central African plateaux, the campo cerrados of Brazil, and the monsoonal tallgrass woodlands of Australia. Because of the high rainfall and prolonged wet season, water is seldom limiting, even on stony or lateritic soils, other than on a seasonal basis. The grasses are tall, fibrous, and of low nutritional quality. Grass production is highest in the open, between trees. Grasses growing under trees benefit from the more mesic conditions and higher nutrient status of the soils but produce less biomass than grasses growing in the open. This abundance of low-quality plant material, in Africa at least, supports only a low biomass and diversity of large herbivores. The amount of plant matter that they consume annually is generally low, though periodic outbreaks of lepidoptera larvae, one of the characteristic features of these systems, can cause severe defoliation.
Most primary production goes into an increase in standing crop biomass or is recycled as litterfall. Litter quality is low and decomposes rather slowly in the absence of fire. The decomposer biomass, particularly of termites and, in the wetter savannas, earthworms, is very high and may equal or exceed that of primary consumers. Dry season fires occur regularly and are fuelled by often large amounts of dead or dry material which has accumulated by the end of the growing season. Fires are sufficiently intense to kill seedlings and saplings, thereby eliminating fire-sensitive species. However, fire is seldom able to control all woody plant establishment and growth. Once established, many woody species are able to survive these fires by resprouting from extensive underground root systems (Frost 1984).

The presence of a high underground biomass and the maintenance of substantial carbohydrate and nutrient reserves, together with the ability to resprout if damaged, means that the woody plants in these systems are well buffered against periodic disturbance in the form of fire, drought and the occasional outbreak of herbivorous insects. The systems are therefore relatively stable. If subjected to disturbance, such as the clearing of woodland for cultivation, they tend to revert to woodland once the source of disturbance has been relieved, though this may take some time, particularly if there has been a loss of woody plant propagules (Robertson, pers. comm.). The rate of recovery depends largely on the extent of decline in the organic matter pool and therefore on the nutrient status of the system following clearing.

Two other functionally distinct but less widespread systems occur. The first consists of low-medium quality grasslands with few woody plants. These are found in areas where both water and nutrients are limited. They usually occur under relatively high rainfall on sites with shallow soils (for example, some of the upland plateaux of Central Africa, campo sujo and campo limpo grasslands in Central Brazil, and parts of the llanos of Venezuela), or under lower rainfall on nutrient-poor sands (for example, the southern Sahel). In Africa, such areas support a low biomass of fibre-tolerant, and species- and plant-part selective grazers. The density of herbivores is generally too low to reduce the biomass of grass sufficiently to exclude dry season fires, where these occur. These fires limit the establishment of woody plants, but have little effect on the grasses, most of which are dormant at the time. Because of the relatively low plant production, soil organic matter levels are often low. Any reduction in input resulting from excessive herbivory or fire leads to a decline in the amount of organic matter which only recovers slowly because of the low level of plant production.
Secondly, there are areas in which neither water nor nutrients are limited. These occur in some Rift valley situations in Africa, and along the foothills of the major escarpment zones. The vegetation consists primarily of medium-high quality woodland with palatable grasses. In Africa, such systems support a high biomass and diversity of both fibre-tolerant and selective grazers and browsers. These are potentially the most unstable of savanna systems (Bell, 1984). If disturbed, for example by the destruction of the woody canopy, they change rapidly to one of a number of alternate states which can be maintained by a combination of fire, plant competition for water, and the type and intensity of herbivory.

For example, where woody plant density is reduced, grass production increases, as does the amount of water used by the grass layer. This may reduce the amount available to trees and so limit their growth. Subsequent changes depend on the quality of the grass after tree clearing. If grass quality is low then fibre-tolerant herbivores will be favoured. However, these species seldom reduce the amount of grass sufficiently to exclude fires. The regeneration of woody species is inhibited and an open grassland maintained.

If the grass quality is relatively high, then smaller, more selective grazers will be favoured. These species can reduce the biomass of grass sufficiently to lower both the frequency and intensity of fires. The system may stabilize at this point, with a high biomass of grazers and a high production but low biomass of grass. However, if the competitive pressures exerted by grasses on woody plant seedlings are periodically reduced, for example by the combined effects of heavy grazing and drought, or if the climate and soils favour the growth of trees, then woody plants will gradually re-establish and eventually suppress grass production.

Where conditions do not favour the rapid growth of woody plants, browsers alone can sometimes check their increase. More usually, browsers and fire interact. Regular fires maintain woody plants within the reach of browsers and in a nutritionally acceptable state (Trollope 1974). The low biomass of woody plants favours the growth of grasses which in turn provide fuel for later fires. Occasionally, fire and browsing are unable to check the increase in woody plant biomass, for example, during a series of very dry years. Woody plants may then increase to the point where they can suppress grass growth, thereby reducing both fuel loads and fire intensities.

HUMAN INFLUENCES

Humans have been associated with savannas for a long time, as hunters, pastoralists and cultivators. Their current influence is widespread and involves a range of land-use practices which modify savannas to varying degrees (Table 1). Some of these activities,
such as wood harvesting and the clearing of land for cultivation, have direct effects on soil structure and fertility, the cycling of nutrients, and on the composition of vegetation (UNESCO, 1979). Other activities, such as the use of fire, the hunting of wild herbivores, and the keeping of livestock, affect the soil and vegetation indirectly. For example, increasing cattle numbers leads to greater grass consumption, less plant cover, increased trampling and compaction of the soil, decreased infiltration, greater runoff and erosion, less plant available moisture, and increased aridification of the soil. The reduced grass growth also results in fewer, often less intense fires and less competition for woody plant seedlings, in some cases leading to marked increases in the density of these species.

Table 1. Types of land-use in savannas and the degree to which these modify savanna structure and functioning.

<table>
<thead>
<tr>
<th>Land use</th>
<th>WILDLIFE CONSERVATION</th>
<th>WOOD HARVESTING</th>
<th>PASTORALISM Nomadism Transhumance</th>
<th>WOOD HARVESTING</th>
</tr>
</thead>
<tbody>
<tr>
<td>Degree of modification</td>
<td></td>
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<td></td>
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<tr>
<td>Minimum</td>
<td>Protected Areas (e.g.</td>
<td>Nomadism Transhumance</td>
<td>Timber Fuel</td>
<td>Shifting cultivation</td>
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<td></td>
<td>National Parks)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Medium</td>
<td>Game Ranching</td>
<td>Ranching Timber Charcoal</td>
<td>Conventional agriculture - dry land cropping</td>
<td></td>
</tr>
<tr>
<td>Maximum</td>
<td>Domestication Cultivated pastures: Afforestation Irrigated crop production zero grazing</td>
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Increasing development---------

Savannas on the different continents have been exposed to these impacts for very different lengths of time and this may be reflected in their present structure. Moreover, with the sharp increase in the human population, the intensity of many of these impacts has increased markedly in recent times. In the dry savannas especially, the combined effects of high animal numbers and reduced plant cover,
Regimes.

Understanding the details of the water, nutrient, fire and herbivory
the particular land-use history of an area is as crucial as
now a major determinant of many of the observed patterns. Knowing
present-day savannas, we need therefore to recognize that humans are
atept to understand the structure and functioning of

V. Arthur and productivity of the system.

soil, water and vegetation, and leading to a sharp decline in the
below-average rainfall, creating even greater pressures on the
particularly during droughts, have led to apparent irreversible

change.
SECTION III: HYPOTHESES ABOUT THE RESPONSES OF SAVANNAS TO STRESS AND DISTURBANCE

INTRODUCTION

The underlying motivation for this programme is the need to improve savanna management. Two issues are of major concern: (1) alterations to the ecological structure of savanna communities, involving changes in species composition, relative abundance and relationships between species; and, (2) changes in functioning, principally declines in productivity, resulting from changes in water and nutrient availability. To understand the implications of these changes for the dynamics of savannas, and therefore for their management, four key questions have been posed. In attempting to answer these questions, we propose that the main research programme be concentrated on testing a number of related hypotheses. These will serve to focus the research effort rather than have it dissipated across a spectrum of unrelated projects which, while interesting in their own right, do not substantially advance our understanding of savanna dynamics in ways which would lead to improved management.

The list of hypotheses is clearly incomplete. It is likely that some important aspects of savanna ecology have not been included because we currently do not know enough about them. These poorly understood components and processes will need to be investigated within the broader framework of the programme. The resulting knowledge can then be used to refine the existing hypotheses or to propose new ones. The revision and formulation of hypotheses in the light of new observations and insights will be one of the objectives of the series of workshops to be held during the course of the programme.

FUNCTIONAL CLASSIFICATION OF SAVANNAS

Savannas encompass a wide variety of systems with different structural and functional characteristics. This makes classification difficult. Existing classifications, based primarily on physiognomy, are unsatisfactory since they do not convey much about function. Moreover, most of the schemes are regional or, at best, continental in scope. None are accepted world-wide. A general structural-functional classification of savannas is therefore urgently needed.

We consider that soil moisture and nutrient availability are the primary determinants of savanna functioning. Their wide variation is probably a major reason for the diversity of savanna types. However, simple indices of moisture and nutrient availability based on, for example, mean annual rainfall and soil type, do not adequately explain all of this diversity. Better measures of plant-available moisture and nutrients are therefore needed before a structural-
A functional classification of savannas can be produced. Some of the factors that should be taken into account are: solar radiation; air temperature; seasonality, predictability and variability of rainfall; soil texture; pH; cation exchange capacity; nutrient mineralization rates; topography, and land-use history.

A possible index of moisture availability is the degree to which evaporative demand is met by soil water: the ratio of actual to potential evapotranspiration might be appropriate. Such an index would integrate solar radiation, air temperature, rainfall, soil texture, topography and seasonality. An index of soil nutrient availability could be the mineralizable capacity of the soil, with special emphasis on nitrogen and phosphorus. Allowance may have to be made for other soil factors which could affect the vegetation (e.g. exchangeable aluminium and sodium percentages, the presence of heavy metals, and shortages of micronutrients).

We propose to develop these two indices to produce a classification of the world’s savannas based on an ordination of actual sites in relation to these indices. The prediction to be tested is that sites with similar moisture and nutrient indices will exhibit similar structural and functional characteristics.

In the current absence of a satisfactory classification, we have used the following hypothetical arrangement of savanna types within the Plant Available Moisture (PAM) and Available Nutrients (AN) plane (Figure 2) as a basis for formulating some of the hypotheses.

Figure 2. Hypothetical distribution of savanna types in relation to the main determinants of savannas (modified from Bell, 1984)
HYPOTHESES

Each of the following hypotheses is presented in three parts: (i) a statement of the hypothesis, with brief amplification where necessary; (ii) a statement of its implications for management; and (iii) an indication as to how the hypothesis might be tested.

Hypothesis 1

Changes in savanna composition and production, induced by the same proportional change in plant available moisture and available nutrients across the PAM/AN plane, will be greater with decreasing amounts of both.

Given the assumption that moisture and nutrient availability are major determinants of savanna functioning, the expectation that changes in PAM and AN cause a proportionately greater change in plant production in those systems where both are most strongly limiting is relatively straightforward. It is less obvious why a similar trend should be expected of changes in species composition. It is based on assumptions that PAM and AN vary more in arid, nutrient-poor systems, and that the species in these systems differ widely in their capacities both to survive prolonged periods of water and nutrient stress and to exploit occasional pulses in availability. Changes in PAM and AN in such systems are more likely to result in changes in the dominant species than in those systems where moisture and nutrients are more readily available and conditions for growth more favourable.

Implication

The main implication for management is that actions which affect the availability of water and/or nutrients are going to have proportionately greater effect in those systems in which PAM and AN are most limiting. These effects will result not only from actions which increase PAM and AN, such as irrigation and fertilization, but also from ones which indirectly lower them, for example, harvesting, the use of fire, and overstocking. There are also implications for monitoring. Attention needs to be focused on the possible effects of management actions on the physical environment, particularly in strongly water- and nutrient-limited systems.

Test

The hypothesis can be tested by comparing the responses of different savanna types in the PAM/AN plane to changes in water and nutrient availability (e.g., through irrigation and fertilization, both singly and in combination) and monitoring the resulting changes in species composition and production in each case. The hypothesis predicts that the magnitude of change will be greatest in those systems in which both water and nutrients are most limiting.
Hypothesis 2

The co-occurrence of two or more independent events (e.g., drought, above-average rainfall, frost, fire, herbivory) will have synergistic effects in changing savanna structure and production.

In terms of this hypothesis, marked shifts in composition or abundance are often caused by the co-occurrence, or close sequence, of events with compounding effects. For example, the establishment of woody plants may depend on the co-occurrence of (i) a period of exceptionally high or out-of-season rainfall; (ii) reduced competition from perennial grasses; (iii) low herbivore pressure; and (iv) a period without fire. From a management perspective, some of these events are manageable (e.g., fire, herbivory); others are not (e.g., above-average rainfall, droughts, frost).

Implications
If this hypothesis is valid, then management aimed at inducing, or avoiding, major changes in community composition may only be possible when two or more independent events coincide. Additionally, events which co-occur infrequently are likely to induce greater shifts in vegetation composition and production. Understanding the effects on key species of interactions between particular climatic, fire and herbivory events, and knowing the probabilities of co-occurrence of these, is a prerequisite for effective management.

Test
A test of this hypothesis would be to impose a variety of stresses or disturbances on a community, singly and in combination, and then monitor the subsequent changes in species composition, relative abundance and production. Since any changes that occur are going to reflect differences between species in establishment, growth, recruitment and mortality, a study of these processes will be essential for understanding the mechanisms of change. In any between-site comparisons, the history of each site will have to be taken into account.

Hypothesis 3

Any substantial change from the prevailing frequency, intensity or sequence of events in a savanna will result in a marked change in structure and production.

Implications
Relatively rigid fire or herbivory regimes are often applied by management. One consequence of this is that communities eventually become dominated by those species which are best able to accommodate the prevailing stress and disturbance regimes. Species which are
better adapted to other regimes decline. Any substantial deviation from the prevailing regime generally results in sudden changes in species composition and production, the magnitudes of which are related to the degree of change in the regime. By maintaining a variable herbivory or fire regime, and thereby regularly exposing the species within the system to a wider range of conditions, managers can increase the resilience of the system to these disturbances and minimize the risk of sudden shifts in composition and production.

Test
The hypothesis can be tested experimentally by changing variable and fixed herbivory or fire regimes and monitoring the resulting changes in species composition and production. The hypothesis predicts that the greatest change will occur in those cases where a regime has been most rigidly applied and where the difference between the original and the new regime is greatest.

Hypothesis 4

Changes in savanna structure and function arise from changes in the seasonal timing and pattern of one or more environmental stresses, independently of the degree of stress.

Implications
This introduces the element of the timing of events as a factor in savanna dynamics. The effects of stresses such as fire, frost or herbivory often depend on the phenological state and physiological condition of the plants at the time. Plants which are dormant are usually less affected than plants which are actively growing. A stress occurring at one time of the year may stimulate reproduction whereas at another time it may retard it. The timing of particular management actions therefore may be as important as their magnitude and this needs to be taken into account in management planning. In this regard it is crucial to know what are the critical periods in life cycles of key species and how these might be affected by different management actions.

Test
A test of this hypothesis would involve varying independently the timing and intensity of events such as fire, herbivory or artificial drought, and monitoring the effects of this on the growth, reproduction and survival of individuals of the key species. The hypothesis predicts that changes in species populations will be determined more by the timing of the event, in relation to critical periods in the species' life cycle, than by its magnitude.
Hypothesis 5

Increasing levels of herbivory in single-herbivore systems increases the proportion of unpalatable species in the community.

Hypothesis 5(a)

An alternative to Hypothesis 5 is: Changes in the proportions of palatable and unpalatable species depend more on the time of grazing in relation to the phenology of the species, than on the level of herbivory.

Implications

The underlying principle of Hypothesis 5 is that in systems dominated by one species of herbivore (e.g. cattle), selective feeding by the herbivore changes the competitive balance between the preferred, palatable species and the unpalatable ones in favour of the latter. This effect is thought to be more pronounced at higher grazing intensities. To counter this, a system of controlled selective grazing is often applied. The system is based on lenient use of preferred species and no defoliation of the unpalatable ones, and involves two main assumptions: (i) that production of preferred species is stimulated by moderate defoliation; and (ii) that in the absence of defoliation by grazing or fire, unpalatable species eventually become moribund and decline. An alternative management system, non-selective grazing, is based on the opposite principle. It assumes that moderate defoliation is more detrimental to unpalatable species than heavy utilization is to the palatable ones. Accordingly, high grazing pressures are applied for brief periods in order to force the animals to graze both the palatable and unpalatable species.

The reasoning behind Hypothesis 5(a) is different. For much of the time, grazing does not appear to have much of a negative effect on grasses; their production may even be stimulated. However, defoliation during the early stages of growth is often deleterious. The decline of a species therefore may be largely the result of defoliation during this early growth phase. Relieving the grazing pressure on palatable species at this time may be necessary to maintain their abundance in a sward.

If appropriate grazing strategies are to be defined for different savanna regions, it is essential that these different hypotheses and their assumptions be tested across the range of savannas. Managers need to know how the timing, intensity and frequency of defoliation affect the growth and reproduction of key pasture species (these include both species that decrease and those that increase under grazing), and how this in turn influences their population dynamics and interactions.
Test

The test of these hypotheses can be carried out in conjunction with the test of Hypothesis 4 by varying independently the intensity and timing of grazing, and monitoring changes in the populations of preferred and non-preferred species. Hypothesis 5 predicts that palatable species are increasingly adversely affected by an increase in grazing intensity and that this favours the unpalatable species, enabling them to increase in the sward. In contrast, Hypothesis 5(a) predicts that plants defoliated during the early growth period will be more susceptible than those defoliated when the plants are dormant or have completed most of their annual growth. Any changes in species composition which occur will be caused by differences in the time of defoliation relative to the time of early plant growth.

Hypothesis 6

The effect of disturbance on the rate and extent of change in the species composition of a savanna depends principally on the life-history characteristics and population biology of the species.

The effects of disturbance on the species in a community are usually selective, some species being more susceptible to a particular disturbance than others. Consequently, species composition tends to shift in favour of those species best adapted to survive the particular disturbance, recover from its effects and exploit the post-disturbance environment. Attributes which enable a species to recover rapidly after disturbance include (i) the presence of substantial belowground reserves; (ii) the capacity to resprout; (iii) the presence of relatively large reserves of dormant seeds with variable germination requirements or, alternatively, the capacity to disperse to and recolonize a site rapidly after disturbance; and (v) the ability to establish under extreme environmental conditions.

Implications

Prior consideration of the ways in which different species are likely to respond to particular management actions or environmental events is crucial to effective management. An understanding of the main features of the life history and population biology of key species is therefore necessary. For example, under what conditions do different species establish from seeds, grow to maturity and reproduce? What conditions cause the widespread death of individuals of a species? How are these processes affected by fire, grazing, drought and interactions with other species? Related species do not necessarily respond in the same way to the same management action.
The hypothesis can be tested either by imposing on a community a disturbance such as extreme defoliation, or removal of woody plants, or by studying natural disturbances such as extreme drought and monitoring the resulting changes in abundance and biomass of particular species. The changes need to be studied at the population level in order to understand the mechanisms involved. The species chosen for study should encompass species with a wide array of contrasting life history attributes and, where possible, known differences in response to the particular disturbance.

Since the relationships, if any, between species' life history attributes and kinds of change in the abundance and biomass of these species are multivariate, possible associations can best be displayed through correspondence analysis. The hypothesis predicts that the direction, magnitude and manner of change will be similar in species having similar life-history attributes, whereas species with different attributes will tend to respond differently.

Hypothesis 7

The responses of savanna species to stress can be predicted on the basis of their life history characteristics and population biology.

Some of the attributes which enhance a plant's capacity to withstand stress include: (i) a high reproductive output, particularly one that is stimulated by stress; (ii) a large root:shoot biomass ratio, which limits the amount of material that herbivores or fire can consume; (iii) unpalatability to herbivores, or other features which restrict the amount of foliage consumed; (iv) compensatory growth in response to defoliation; (v) the presence of energy and nutrient reserves on which the plant can draw in times of stress; (vi) the ability to reproduce vegetatively; (vii) morphological and phenological plasticity, which allow rapid adjustments to stress; and (viii) physiological quiescence during climatically unfavourable times of the year.

Implications

Effective management depends on being able to assess the consequences of different actions and choose that which comes closest to giving the desired result. Since it is not feasible to determine empirically the response of all species to every management action, some basis is needed for being able to predict the probable responses of the key species. If this can be done by using information on the species' life-history attributes, then the potential for effective management will be greatly enhanced.
The test of this hypothesis is similar to that of Hypothesis 6 except that the available information on the life-history of the key species is used to predict changes in their abundance and biomass before the experiment is carried out. (At our current level of understanding it is likely that the predictions will only be qualitative.) The test involves making a comparison between these predicted changes and those induced by the particular stress. If the observed changes differ from those predicted then either the life history attributes of a species are not good predictors of population change or our current understanding of these attributes and their effects is inadequate for making accurate predictions.

A direct test of the hypothesis will not be possible where there is insufficient life history information available at the outset. Instead, the information on life history attributes will have to be collected for each species during the course of the experiment. As in the test of Hypothesis 6, correspondence analysis can then be used to detect any underlying associations between specific attributes and particular stress-induced changes in abundance and biomass. The aim would be to distinguish between those attributes which correlate with the observed population or biomass changes (these will be the attributes likely to have predictive value), those which correlate with each other and are therefore redundant, and those which do not correlate with any of the changes.

To determine how successfully actual changes can be predicted, either a reserve set of data (i.e. data from one or more of the replicated plots, withheld from the initial analysis), or an independently collected data set, can then be analysed to see to what extent the identified relationships remain stable and are predictable. However, causality in these relationships cannot be inferred from these analyses. To understand the mechanisms involved will require detailed studies of the ways in which stress affects key population processes in each of the species.

Hypothesis 8

A decrease in the effective rainfall of a site leads to a decline in species diversity as a result of the loss of species with diverse life-history characteristics.

Implications

Management actions which reduce the input of water to the soil (e.g. by overstocking to the point where trampling and compaction of the soil result), or which increase the rate of plant water-use (e.g. by fertilization), may shorten the length of time that water is
available to plants. This will concentrate phenological types in
time, resulting in an eventual reduction in species diversity
through competition and drought-induced mortality. Management
actions which might shorten the period of soil water availability
would have to be avoided.

Test
The hypothesis can be tested by using rain-out shelters and
irrigation to keep constant the total amount of water available to
the plants while varying the period of availability. The hypothesis
predicts that, under the same total amount of plant available water,
there will be marked changes in diversity, including perhaps a loss
of species, in those situations where the period of water
availability is sharply reduced. Species normally developing in the
middle to late rainy season will be most susceptible, while drought-
tolerant species will be favoured.

Hypothesis 9

The stability of savanna ecosystems, in terms of the capacity of
their component species to recover from stress or disturbance, is
strongly influenced by the degree of environmental constraint on
plant establishment and growth.

Recovery from stress or disturbance can be arrested or redirected by
the subsequent intervention of drought, fire, herbivory, etc. before
the process of recovery has been completed. Where recovery is slow,
the likelihood of subsequent events influencing the eventual outcome
is increased.

Implications
The main implication for management is that where the process of
recovery from stress or disturbance is slow, either because of the
severity of the initial stress or disturbance, or because of strong
environmental constraints on establishment and/or growth (e.g.
nutrient-poor soils, low water availability, poor seedbed
conditions, etc.), subsequent events may occur which will affect the
eventual outcome. Where these subsequent events are controllable,
managers would need to ensure that they allow sufficient time for
the species to recover before these other pressures are imposed.
Where subsequent events are uncontrollable and unpredictable, then
the intensity and timing of management actions would have to be
adjusted so that the plants could recover in the shortest time
possible.
Test
The hypothesis can be tested by comparing the patterns of vegetation change (species composition, relative abundance, production of selected species) after disturbance (e.g. artificial drought) on sites which differ in their suitability for plant growth. The hypothesis predicts that where conditions are unfavourable for establishment and growth, the subsequent intervention of events such as fire, herbivory, or further drought will cause greater mortality and changes in species composition and production, than will the same events, occurring at the same time, on more favourable sites.

Hypothesis 10
If disturbed, savanna ecosystems tend to return to their former state. The time taken to return, and the pathways involved, are determined by the magnitude of the initial displacement in species composition or production.

Hypothesis 10(a)
An alternative to Hypothesis 10 is: Stability is not a major feature of savannas. Disturbance-induced changes in species composition and productivity are accommodated by structural and functional adjustments within the community. Autogenic recovery does not occur.

Implications
The concept of stable equilibria is central to much current ecological theory and application. Its relevance in the context of savanna dynamics can be questioned, especially in view of the stochastic nature of most of the driving variables, the interactiveness and non-linearity of many of the processes, and the resulting contingency of many of their effects. Yet the concept is widely applied in savanna management. For instance, attempts by managers to reverse undesirable changes in vegetation composition or productivity caused by, for example, overstocking, involve removing the cause of the disturbance and resting the disturbed area.

The underlying assumption is that species composition and production at a site tend towards a single, stable equilibrium which is determined primarily by the prevailing soil conditions and climate (mainly rainfall). Moreover, if composition and production are disturbed they will return automatically to their predisturbance state. Hypothesis 10 implies that the time required for recovery, and hence the period of rest that is required after disturbance, increases with the increasing magnitude of disturbance (as measured by the initial displacement in species composition or production).
In contrast, Hypothesis 10(a) states that once a savanna has been disturbed, species composition and production do not automatically return to their predisturbance levels but, instead, the changes are accommodated through structural and functional rearrangements. Therefore, in order to restore the previous relationships, another disturbance, acting in the opposite direction, has to occur. Resolving the question of how savannas respond to disturbance has important implications for the kinds of management actions that are required to counter any undesirable changes brought about by disturbance. In both cases, it is clear that regular, frequent monitoring is needed in order to detect and respond rapidly to any adverse changes which might occur.

Test
Both hypotheses can be tested in the same experiment by disturbing adjacent areas to different degrees (e.g. removing different proportions of woody biomass) and monitoring the resulting changes in species composition and production. Hypothesis 10 predicts that composition and production will eventually return to their predisturbance levels, with the time taken being proportional to the magnitude of the disturbance. On the other hand, Hypothesis 10(a) predicts that an area, once disturbed, will not show any consistent tendency to return to the original, predisturbance state unless it is subsequently disturbed in the opposite direction. The system will either remain at the point to which it was disturbed, or undergo further change in the same direction.

Hypothesis 11

The reversibility of change in plant species composition and production is inversely related to the degree of change in soil physico-chemical properties.

Hypothesis 11(a)

An alternative to Hypothesis 11 is: No irreversible change in species composition will occur without a concurrent and long-lasting change, of a particular magnitude, in soil physico-chemical properties.

The assumption underlying both hypotheses is that the physico-chemical properties of the soil are a major determinant of savanna composition and productivity. The distinguishing feature between the two hypotheses is the degree to which plant species composition and production are able to recover from disturbances to soil properties. In terms of Hypothesis 11, any changes to the soil during disturbance results in a corresponding change in the equilibrium
Table 2. Some possible effects of herbivores on soil properties and processes

<table>
<thead>
<tr>
<th>IMPACT</th>
<th>EFFECTS</th>
<th>CONSEQUENCES</th>
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</thead>
<tbody>
<tr>
<td>1. Reductions in plant and litter cover</td>
<td>1.1 Increase in area of bare soil</td>
<td>* Increased insolation</td>
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<tr>
<td></td>
<td></td>
<td>* Increased exposure to raindrop impact</td>
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<td></td>
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<td>* Increased soil temperature</td>
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<td>* Reduced infiltration</td>
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<td></td>
<td>* Increased run-off</td>
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<td></td>
<td></td>
<td>* Increased potential for water erosion</td>
</tr>
<tr>
<td></td>
<td>1.2 Reduction in input of litter</td>
<td>* Lower S.O.M.</td>
</tr>
<tr>
<td></td>
<td>1.3 Reduced root growth</td>
<td>* Less soil cohesion</td>
</tr>
<tr>
<td></td>
<td></td>
<td>* Increased potential for leaching to groundwater</td>
</tr>
<tr>
<td>2. Input of dung and urine</td>
<td>2.1 Change in spatial and temporal distribution of nutrient inputs</td>
<td>* Increased heterogeneity in distribution of soil nutrients</td>
</tr>
<tr>
<td></td>
<td></td>
<td>* Increased volatilization</td>
</tr>
<tr>
<td></td>
<td>2.2 Change in quality of nutrient inputs</td>
<td>* More rapid O.M. turnover</td>
</tr>
<tr>
<td>3. Compaction (increase in bulk density of the soil; most likely when soils are moist)</td>
<td>3.1 Macropore space reduced</td>
<td>* Reduction in soil water-holding capacity</td>
</tr>
<tr>
<td></td>
<td>3.2 Micropore space increased</td>
<td>* Less plant-available water</td>
</tr>
<tr>
<td></td>
<td>3.2 Total pore space reduced</td>
<td>* Less favourable soil microclimate for biota</td>
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<td></td>
<td>3.4 Increased run-off</td>
<td>* Poor environment for seedling establishment and root growth</td>
</tr>
<tr>
<td></td>
<td></td>
<td>* Increased potential for water erosion</td>
</tr>
<tr>
<td>4. Trampling (break up of soil aggregate structure; most likely when soils are dry)</td>
<td>4.1 Reduced size of soil aggregates</td>
<td>* Increased potential for wind and water erosion</td>
</tr>
<tr>
<td></td>
<td>4.2 Formation of soil surface seals</td>
<td>* Potential loss of surface soil</td>
</tr>
<tr>
<td></td>
<td></td>
<td>* Reduced infiltration</td>
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<td></td>
<td></td>
<td>* Increased run-off</td>
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<td></td>
<td></td>
<td>* Loss of soil seed store</td>
</tr>
<tr>
<td></td>
<td></td>
<td>* Unfavourable environment for seed germination and seedling establishment</td>
</tr>
</tbody>
</table>
conditions for plant growth, and this in turn affects the degree to which the vegetation is able to return to its pre-disturbance state. Thus the greater the disturbance to the soil, the less completely the vegetation recovers to its pre-disturbance state.

In contrast, Hypothesis 11(a) implies that below some critical point (which probably differs from site to site, depending on the soil type and climate), any changes in soil properties do not have a lasting influence on plant species composition or production. However, if the soil is disturbed beyond this point, the changes in the plant community become irreversible.

**Implications**

Large herbivores are often implicated in changes to plant species composition and production, both directly, as partially selective consumers, and indirectly, through their impact on soil properties and processes. These include trampling and compaction, reductions in plant and litter cover, and the input of nutrients in dung and urine, all of which have many interlinked consequences (Table 2). One implication of these hypotheses is that the direct effects of large herbivores on long-term vegetation change are likely to be less important than indirect effects.

This has implications for the assessment and monitoring of range condition and carrying capacity in savannas. At present, assessments of the carrying capacity of an area are made almost entirely in terms of the amount of food available for animals, rather than in terms of how much trampling and compaction an area can sustain and what amount of plant cover will be needed to protect the soil. In this respect, more consideration needs to be given to the differences which exist between areas in their susceptibility to degradation (e.g. clayey soils are more easily degraded than sandy soils, particularly when moist).

**Test**

Since large herbivores are often implicated in changes to both soils and vegetation, one test of Hypotheses 11 and 11(a) could involve a multifactorial experiment in which (i) simulated grazing; (ii) trampling and compaction; and (iii) the addition of excreta, are varied singly and in combination to create a series of changes in the soil and vegetation at a site. This would also allow the effects of these different disturbances to be assessed independently of each other. Some of the predicted changes are listed in Table 2. Key variables which need monitoring include surface soil compaction and/or bulk density, infiltration rate, soil temperature, soil organic matter fractions, N and P mineralization rates, as well as changes in plant species composition, root growth, and seedling establishment. These would be monitored during the disturbance and after the treatments have been withdrawn, to determine whether there has been any recovery to pre-treatment levels.
The eventual difference in vegetation composition and production between the pre-treatment and post-recovery periods, and the relationship of these changes to the degree of change in soil properties which has occurred over the same period, provides the basic test of the hypotheses. Hypothesis 11 will be invalidated if the differences in vegetation composition and production are uncorrelated with the degree of change in soil properties. Hypothesis 11(a) will be invalidated either if there is no relationship between the amounts of change in the vegetation and in soil properties, or if the relationship is positive and linear.

Hypothesis 12

A reduction in the diversity of savanna plant communities results in a decline in soil organic matter and a disruption of nutrient cycling processes.

The disruption of nutrient cycling arises from (i) the narrowing of the spectrum of litter quality; (ii) changes in the patterns of root growth in time and space; and (iii) a reduction in synchrony between nutrient availability and demand. These changes may result in the loss of nutrients through leaching, particularly on well-drained soils in regions of high rainfall.

Implications

This hypothesis has two major implications for the maintenance of soil fertility. First, there is an advantage in maintaining phenological and structural diversity in savanna plant communities. Secondly, it is important to maintain those soil biological processes which prevent or reverse the leaching of nutrients, especially where the soils are well-drained and nutrient-poor. Woody plants are crucial in both instances since they produce substantial amounts of low quality litter, which decomposes slowly and contributes to a build-up in surface soil organic matter. They also maintain active root growth and nutrient uptake in the horizontal and vertical planes of the soil profile. The removal of woody plants from a savanna is therefore likely to cause considerable disturbance with long-term effects on nutrient status of the system.

Test

The hypothesis can be tested by comparing nutrient cycling processes in savannas with varying proportions of trees and grass. The following processes need investigating: (i) the timing and quality of different above- and below-ground organic matter inputs; (ii) the decomposition rates of these materials and the resulting patterns of nutrient release; (iii) the extent of nutrient immobilization in, and release from, soil organic matter; and (iv) the seasonal pattern of nutrient uptake by the vegetation. The hypothesis predicts that those communities which are less diverse, particularly in respect of
woody plants, will have less organic matter, smaller amounts of total exchangeable bases, a more rapid turnover of nutrients, and a greater loss, or potential for loss, of nutrients through leaching.

Hypothesis 13

The fertility, production and stability of savannas is maintained by the diversity and activity of soil organisms.

Implications
A change in the functioning of soil organisms tends to modify the rate and direction of nutrient flows in the soil, thereby affecting the availability of nutrients to plants and influencing their productivity and stability. The soil biota can be affected directly by actions such as the use of biocides, or indirectly, through actions which modify either the soil environment or the chemical make-up of organic matter inputs. These include altering the composition of the vegetation (e.g. by changing the proportion of trees and grass, or changing the proportion of nitrogen-fixing plants in the community), and affecting its quality (e.g. through fertilization). More consideration needs to be given to the consequences of such actions, particularly where soil fertility is apparently closely linked to the dynamics of soil organic matter.

Test
This hypothesis can be tested by manipulating the activity and/or abundance of soil organisms, both through the use of biocides and by changing the nature of organic matter inputs to the soil. The resulting changes in both soil biological activity (including the rates of decomposition and mineralization of litter and soil organic matter, and the rate and timing of nutrient release in relation to the timing of plant nutrient demand), and changes in plant species composition and production, would be monitored. Some of the variables to be measured include: litter standing crop and soil organic matter levels, their rates of decomposition and mineralization, total and mineral N, available P, as well as features such as soil bulk density and rainfall infiltration rates which are indirectly affected by soil biological activity.

Hypothesis 14

Woody plants contribute more to functional stability in dystrophic than in eutrophic savannas.

Features of woody plants that provide inertia to change and which, therefore, contribute to increased stability include: (i) higher individual biomass and greater longevity of woody plants; (ii)
conservative growth patterns and the slow turnover of organic matter and nutrients; (iii) large root:shoot ratios limiting the amount of material which can be consumed by herbivores or fire; (iv) the capacity to respout after disturbance; (v) the capacity to take up nutrients from deep in the soil profile, which counters the effects of leaching; and (vi) an increase in the total amount of nutrients cycling in the system, thereby influencing the productivity and species composition of the grass layer. Woody plants also provide a highly predictable dry-season food source for browsing ungulates. The significance of all these features is likely to be greatest in systems where nutrients are most limiting.

Implications
A reduction in the woody component of savannas is likely to result in changes to the soil microclimate, the quality of litter inputs, soil organic matter levels and mineralization rates, and a greater potential for nutrients to be leached out of the soil profile. These changes may eventually lead to a reduction in the nutrient status of the system and a decline in stability, particularly in dystrophic savannas. Maintaining a high woody plant biomass should therefore be a priority on nutrient-poor sites. Where woodland is cleared from these sites, a proportion of the woody plants should be left to ensure the maintenance of processes such as the recycling of nutrients from deep in the soil profile.

Test
Since even a partial removal of trees from a savanna results in a short-term increase in nutrient availability, because of the increased decomposition of below-ground organic matter, this hypothesis will have to be tested at sites where different densities of woody plants have been artificially maintained for some time (e.g. woodland clearing trials). The hypothesis can best be tested by comparing differences in the amounts of litter and soil organic matter, total exchangeable bases, total and mineral N, available P, soil moisture regimes, and fluctuations in herbaceous composition and production, on adjacent sites with different densities of woody plants.

Specific predictions are that those plots with a higher woody biomass will have: (i) more constant herbaceous composition and production; (ii) higher amounts of litter and soil organic matter; (iii) more total nutrients and higher amounts of the exchangeable bases; and (iv) more favourable soil moisture conditions. Moreover, the effects of a lower woody plant biomass, in terms of changes in the above variables, will be greater on the dystrophic soils.
Hypothesis 15

The compositional and functional stability of savannas increases with an increase in both the diversity of rooting systems and the proportion of plant biomass located below ground.

Implications
Savanna plants generally have extensive root systems and high root:shoot ratios. Although available information on the structural and functional diversity of these root systems is limited, features such as the coexistence of grasses and trees, and the diversity of growth form and phenological behaviour among species at a site, suggest considerable spatial and temporal partitioning of water and nutrient uptake within the soil profile. In those systems with a high diversity in root distribution and functioning, any change in the patterns of water and nutrient availability are likely to be rapidly accommodated, thereby tending to maintain functional stability.

Compositional stability may also be linked to the diversity of root systems and the amount of underground biomass. Plants with a large proportion of their biomass below ground will be less affected by aboveground disturbances. Species with extensive root systems can take up water and nutrients over a wide area and from deep in the soil profile, enabling them to continue functioning even during prolonged drought. Extensive root systems probably also act as energy and nutrient stores, buffering the plants against the effects of a variable climate, frequent fire and herbivory, and enabling them to recover rapidly if disturbed.

The main implication for management therefore is that in systems where a high proportion of plant biomass is located below ground, the plants are likely to be less sensitive to, and quicker to recover from, disturbance. If stability is desired, then actions which would reduce the diversity of that community, or lower the proportion of underground biomass, need to be avoided.

Test
Given the difficulties of excavating root systems and studying their functioning, this hypothesis will be difficult to test. One possible test involves comparing changes in woody and herbaceous species composition and biomass, together with changes in soil moisture and nutrient regimes, at different sites subjected to the same disturbance (e.g. tree-felling). The hypothesis predicts that those systems having the highest proportion of biomass belowground, and the most uniform distribution of roots in the soil profile, would show the least change in species composition, water regime and nutrient loss. They would also be expected to recover more rapidly from the disturbance.
Hypothesis 16

Under similar conditions, the compositional stability of the herbaceous layer in those savannas dominated by annuals and short-lived perennials will be lower than that of savannas dominated by long-lived perennials. Their resilience though will be greater.

Implications

Long-lived perennial grasses are morphologically and physiologically better buffered against temporal fluctuations in resources than are annuals, as a result of having higher belowground carbon reserves and a higher potential for osmotic adjustment in times of stress. They are therefore less likely to be affected by climatic fluctuations, fire or herbivory. In contrast, annuals have to re-establish themselves in a community each year. This makes them more susceptible to any factors which might affect the processes of germination and reproduction. Their populations therefore are likely to be less constant from year to year. In those savannas containing a high proportion of annuals and short-lived perennials fairly rapid changes in composition can be expected. Where stability in the composition of the herbaceous layer is desired, management should aim to maintain a vigorous perennial grass component in a community, particularly in savannas subjected to frequent stress.

Test

The hypothesis can be tested by subjecting areas with different proportions of annuals and perennials to simulated drought or above-average rainfall, fire, or herbivory. The hypothesis predicts that the change in species composition and the seasonal fluctuations in production will be greater in those areas dominated by annual plants. However, in these systems species composition and production will adjust more rapidly to disturbance.

Hypothesis 17

The functional stability of the herbaceous layer in grazed savannas is proportional to the number of grass species present and to the degree of spatial heterogeneity of the vegetation.

Hypothesis 17(a)

Since the diversity of growth form and phenology tend to covary with species number, an extension to Hypothesis 17 is: the stability and productivity of the herbaceous layer in savannas is related primarily to the diversity of plant growth strategies rather than to the number of species.
Most herbivores feed selectively to some degree. Their impacts therefore are seldom spread uniformly across all the plants in a community, with the result that as the abundance or biomass of a grazed species declines, an opportunity is created for other, ungrazed species to increase. The extent of this compensation depends on the amount of overlap between plants in their use of resources, and on the degree to which these resources are limiting. Both are likely to be higher in species-rich communities. Furthermore, some grazers become increasingly selective as both the number of plant species and the heterogeneity of the vegetation increases. This leaves more species able to expand as the grazed ones decline. Accordingly, where there are many species in a community, there is likely to be more competitive release, with the expansion of one suite of plants counterbalancing the decline in others. This promotes functional stability (constancy of production) in species-rich communities in spite of considerable fluctuation in species composition (McNaughton, 1977, 1985).

More generally, wherever specific differences in growth form, phenology, physiology etc., result in species either not being affected equally by an environmental change, or responding differently to that change, a situation exists in which some species are able to expand as others decline. Therefore, in systems experiencing marked fluctuations in environmental conditions (e.g. variations in rainfall, grazing pressure, fire intensity, etc.), the functional properties of the system are likely to be more stable where there is a greater variety of adaptive types present. Although this relationship can exist independently of the number of species in a community, the diversity of adaptive traits will usually be highest where there are many species present.

Implications
Diverse plant communities tend to be more resistant to climate- and herbivore-induced stresses. One of the objectives of management in areas which regularly experience these sorts of stresses should be to maintain a rich and diverse plant community. This would promote a more stable plant cover and production, even though species composition might fluctuate considerably.

Test
These hypotheses can be tested by imposing a heavy grazing pressure on grasslands in which there are different numbers of species. Hypothesis 17 predicts that the change in production and standing crop will be less on species-rich than on species-poor plots, whereas the change in species composition will be greater. Moreover, for plots with similar numbers of species, production will be most stable on those plots with the highest pattern diversity (spatial heterogeneity). In contrast, Hypothesis 17(a) predicts that for plots with similar numbers of species, standing crop biomass and production will be most stable on plots with the greatest diversity of plant growth forms and phenological behaviour.
Hypothesis 18
Savannas in which a high proportion of plant material cannot be consumed, or which is consumed only to a limited extent, are more stable because the individuals are more resistant to defoliation-induced stress.

Implications
The main implication of this hypothesis is that not all uneaten or inedible plant material is necessarily undesirable. The presence of these unutilized species prevents the plant cover from being overutilized and the soil from being exposed and excessively disturbed. Conversely, any management action which increases the proportion of plant cover being consumed, such as supplementary feeding or the re-inforcement of natural pastures with alien forage species (such as legumes), is likely to have a destabilizing effect. This is because as nutritional limitations on the animals are lifted, it becomes possible for them to utilize lower quality forage and, therefore, to be stocked at a higher rate. The resulting lower plant cover and higher animal numbers can eventually lead to degradation of both the vegetation and the soil.

Test
The hypothesis can be tested by comparing changes in species composition, abundance and biomass, and changes in soil physical properties, on grazed plots containing different proportions of palatable and unpalatable plant species. The main prediction is that the changes in species composition and the changes in soil properties, will be less marked in areas with a higher proportion of unpalatable (unexploitable) plant biomass.

Hypothesis 19
Both the compositional and functional stability of savannas increase with an increase in large herbivore diversity.

Implications
It is often argued that domestic livestock do not utilize savannas efficiently, and that by stocking with a variety of wild herbivores (with or without domestic livestock), a higher animal biomass and greater secondary production could be sustained. This argument is based on the idea that wild herbivores generally have different and complementary food preferences (though the available information indicates that different species overlap considerably in their diets). It is also assumed that a multi-species herbivore community utilizes the vegetation more uniformly, thereby keeping the balance between the various components of the vegetation.
These assumptions need to be tested since they have been used as the rationale for many of the mixed domestic and wild herbivore ranching schemes in Africa. The important implications are not only whether the assumptions are correct, but under what conditions they hold. More particularly, are there optimum combinations of species, in terms of proportions of different feeding types, for given ecological situations?

Test
The hypothesis can be tested by manipulating herbivore diversity and monitoring the effects of this on both plant and animal species composition, abundance and production. Because of the size of the areas involved, it is likely that the tests will have to involve comparisons between sites. In this case, possible differences in land-use history, particularly as these might have affected the vegetation, need to be considered.

Hypothesis 20

The species composition of savanna vegetation is a determinant of animal production.

Implications
Domestic livestock management, at least in southern Africa, assumes that animal performance is a function of the species composition of the vegetation, and that it will be higher in regions dominated by better quality, more nutritious plants. Implicit in this view is the idea that differences in plant quality and palatability are a function of the seral status of the vegetation. In this regard, so-called 'climax' communities are presumed to represent the optimum in range condition, and considerable management activity is directed at maintaining or restoring dense stands of palatable perennial grasses in order to enhance or improve animal production. However, there is some evidence that the productivity and digestibility of 'subclimax' and 'pioneer' species can be as high as that of the 'climax' species. A critical test of the hypothesis and its assumptions is clearly needed.

Test
The hypothesis can be tested by comparing forage intake (quantity and quality) and the resulting daily body mass gains of animals (e.g. cattle) being stocked on areas which differ widely in plant species composition. The animals need to be stocked at a sufficiently high density to ensure that they utilize the vegetation fully. The null hypothesis is that daily body mass gains will be independent of the species composition of the vegetation.
SECTION IV: PROPOSED PROGRAMME

OBJECTIVES

This document has been developed over a period of two years involving three workshops (Brisbane, Paris, Harare). In its present form it provides the framework for the initiation of the research programme. The general review and specific hypotheses identify a variety of biological processes which we predict determine the structure and functioning of savannas. Some of these processes are well understood but others (perhaps the majority) are not. The link between management practices and certain desired effects may be well established at an empirical level (the use of fire, for example), but in many cases it is only incompletely understood why such management practices work. Moreover, we do not always know if these are the most desirable or effective practices. Our ability to predict the consequences of management, and of disturbances in general, is very limited.

It is therefore proposed that a programme of collaborative research on savanna ecosystems be mounted to investigate what we perceive to be the major deficiencies in our current knowledge and understanding of these ecosystems. The four components of the programme are:

1. To improve communication and interaction between savanna ecologists, as well as between ongoing research programmes;

2. To promote short term collaborative projects aimed at solving individual key questions;

3. To organize and carry out an intercontinental, comparative experiment on the responses of savanna ecosystems to stress.

4. To incorporate research results into the management of savannas.

PROCEDURE

1. Improving communication between savanna researchers

In spite of the fact that several international conferences on savannas have taken place during the last ten years, better communication between savanna ecologists is badly needed. This can be achieved in a number of ways. We propose the following three steps:

a. Organizing regular symposia and workshops. These will be held on a rotating basis at different research sites and will provide regular opportunities for savanna ecologists to discuss and
synthesize ongoing and completed work, identify unresolved research questions, and formulate new hypotheses and approaches for dealing with them. It will also provide an opportunity for savanna researchers to obtain first hand experience of different systems.

b. Publishing a newsletter. This will serve to promote and maintain contact between savanna researchers and inform them of ongoing activities. It can also serve as a means of disseminating ideas and research results rapidly and in an informal setting. Furthermore, by distributing the newsletter widely, other interested persons and institutions can be recruited into the programme. Dr Patricia A. Werner (CSIRO Division of Wildlife and Rangelands Research, Darwin Laboratories, P.M.B. 44, Winnellie, N.T. 5789, AUSTRALIA) has agreed to serve as the first editor of the newsletter.

c. Maintaining a register of projects and researchers working on savannas. This will enable researchers to identify others who have similar interests, thereby providing the opportunity to establish contact and exchange ideas and experiences.

2. Promotion of short term collaborative projects

From time to time, specific questions relating to savanna structure and function will be identified which will require particular observations and experiments. These projects can be carried out at the main study sites or elsewhere, in which case they would provide an opportunity for the participation of researchers who, because of geographic location, are not able to participate directly in the intercontinental comparisons. This component of the programme will also enable ongoing research projects in isolated areas to be integrated into the overall programme if those researchers so desire. Finally, these special collaborative projects will provide important opportunities for training young researchers. Every effort should be made to help in the design and financing of such projects.

3. Intercontinental comparisons

The core of the programme will be an intercontinental, comparative experiment on the responses of savannas to stress and disturbance. The effects of varying the four principal determinants of savannas, that is, soil water availability, soil nutrient status, herbivory and fire, will be studied at different sites using similar methodologies and approaches. The aim of this is to test the specific and general hypotheses proposed here, to evaluate old management practices and, where possible, suggest new ones.
There is a need for comparable data from a range of savanna sites. Careful consideration must be given to identifying what features need to be measured, how often and when. One of the problems with much of the current savanna research literature is that data on many of the key features of these systems is either lacking or is presented in ways that make it difficult to draw meaningful comparisons.

Wherever possible, the approach will be primarily experimental. Some observations and description are inevitable but, given the limited time-span of the programme, there is a premium on obtaining the necessary information and understanding in as short a time as possible. This is more likely to be achieved by adopting an experimental approach aimed at testing one or more hypotheses than by pursuing detailed descriptive studies.

Both inter- and intra-continental comparisons will be needed. This will involve identifying sites with similar physical environments on different continents, as well as sites with different physical environments and/or land-use histories located on the same continent. In establishing such research centres, preference should be given to sites where there is ongoing research and an existing data base.

4. Incorporation of research results into management

Achievement of this objective requires a two-way flow of information. In order that the results of the programme address the issues of real concern, researchers need to be made aware of the manager's problems and his perceptions of how to solve these. Secondly, the results of the research need to be communicated to the whole spectrum of decision-takers, from the national level to that of the individual manager.

The first of these requirements will be approached through the establishment of a research programme comprising sociologists and resource economists. This group will be represented at all meetings and workshops and will act as the conduit between managers and researchers. The second requirement, extension of research findings, will be approached in a number of ways, from special publications to workshops on savanna management. A central theme will be the development of expert systems for a number of specific management issues in particular regions. The development of an expert system has the dual advantage of guiding research and being a valuable management aid which can be left behind with the users at the completion of the project.
ORGANIZATION

The detailed programme will be organized and coordinated by a Coordinating Committee with the assistance of a Scientific Advisory Committee.

The following have agreed to serve on the Coordinating Committee:

Professor B.H. Walker (Chairman), Australia, for AUSTRALASIA
Dr E.L. Edroma, Uganda, for AFRICA
Professor S.J. McNaughton, USA, for NORTH AMERICA
Professor E. Medina, Venezuela, for SOUTH AMERICA
Dr J-C. Menaut, France, for EUROPE

Ex officio
Professor O.T. Solbrig, IUBS
Dr M. Hadley, UNESCO/MAB

Executive Secretary
Dr T. Younes, IUBS

The functions of the Coordinating Committee will be:

1. To oversee the planning and execution of the programme, including the drawing up of detailed proposals describing the aims, rationale, approach and provisional timetable for the programme.

2. To establish contact with potential contributors to the programme and invite their participation in it.

3. To coordinate the major activities of the programme through organizing workshops and regional meetings.

4. To appoint a Scientific Advisory Committee to assist with scientific matters.

5. To decide on the funding required for organizing and administering the programme at different stages of its development, and drawing up motivations to this effect.

6. To liaise with the IUBS 'Decade of the Tropics' committee and UNESCO's 'Man and the Biosphere' programme.

7. To establish and promote contact with other relevant research programmes such as the Decade of the Tropics programme on Tropical Soil Biology and Fertility (TSBF).
So far, the following scientists have agreed to serve on the Scientific Advisory Committee:

Dr D.H.M. Cumming, Zimbabwe
Mr P.G.H. Frost, South Africa
Dr G. Goldstein, Venezuela
Dr S.K. Imbamba, Kenya
Dr G. Maloof, Kenya
Dr J.J. Mott, Australia
Dr R.W. Ruess, USA
Dr J.F. Silva, Venezuela
Professor M.J. Swift, Zimbabwe

Other members, representing particular disciplines, will be appointed at a later date.

The functions of the Scientific Advisory Committee will be:

1. To advise the Coordinating Committee on scientific matters.

2. To assist the Coordinating Committee in the planning and running of workshops.

3. To assist the Coordinating Committee in preparing detailed guidelines for the scientific phases of the project.

4. To provide on-site advice on behalf of the Coordinating Committee, particularly in the choice, establishment and running of the experimental sites.

FUTURE ACTIVITIES

The following activities are being planned:

1. Distribution of this document to the savanna research community, together with an invitation to participate. The responses will be collated prior to establishing the network of research sites.

2. Publication of the newsletter. All contributions are welcome, particularly news of forthcoming meetings, information on planned, on-going or completed research projects, recent publications, and personal views on the nature, direction and application of savanna research. Contributions should be sent to:

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Australia
3. Compilation of a register of savanna researchers, their research interests and current projects. Details have still to be worked out. A bibliography of savanna research is being compiled.

4. A workshop on programme design and methodology will be convened in France in June 1986.

5. The first of a series of regional workshops is being planned for South America in 1987.

6. A second regional workshop will be held in Australia in 1988, to coincide with the IUBS General Assembly meeting being held there at the same time.
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INDIA - Indian National Science Academy
IRAQ - Scientific Research Foundation
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ISRAEL - Academy of Sciences and Humanities

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LEBANON - Conseil National de la Recherche Scientifique
MEXICO - Consejo Nacional de Ciencia y Tecnología
MONACO - Centre Scientifique de Monaco
NETHERLANDS - Koninklijke Nederlandse Academie van Wetenschappen
NEW ZEALAND - The Royal Society of New Zealand
NORWAY - Det Norske Videnskaps-Akademi
POLAND - Academy of Sciences
ROMANIA - Academy of the Socialist Republic of Romania
SOUTH AFRICA - Council for Scientific and Industrial Research
SPAIN - Consejo Superior de Investigaciones Científicas
SUDAN - National Council for Research
SWEDEN - Kungliga Vetenskapsakademien
SWITZERLAND - Société Helvétique des Sciences Naturelles
TAIWAN - Academy of Sciences
UNITED KINGDOM - The Royal Society
U.S.A. - National Research Council
U.S.S.R. - Academy of Sciences
YUGOSLAVIA - Union of Biological Sciences